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A Monograph of the Genus *Eperua* (Leguminosae: Caesalpinioideae)

RICHARD S. COWAN



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ABSTRACT

Cowan, Richard S. A Monograph of the Genus *Eperua* (Leguminosae: Caesalpinioideae). *Smithsonian Contributions to Botany*, number 28, 45 pages, 13 figures, 2 tables, 1975.—All available data are brought together in a monographic treatment of the legume genus *Eperua*. Eighteen taxa are considered of which four are described as new: *E. duckeana*, *E. obtusata*, *E. grandiflora* ssp. *guyanensis*, and *E. jenmanii* ssp. *sandwithii*. Also one new combination is made: *E. glabriflora* (Ducke) Cowan. In addition to gross morphology, anatomy of leaf epidermis and palynology of most of the species are presented for the first time. Pollen morphology is particularly instructive with respect to the classification derived principally from vegetative and floral morphology.

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A Monograph of the Genus *Eperua* (Leguminosae: Caesalpinioideae)

Richard S. Cowan

Introduction

During an expedition to the upper Orinoco Basin in 1950–51, I first saw living material of the genus *Eperua* and was impressed by the beauty of the flowers and the anomalous pseudotubular corolla. In the years that followed I had occasion to work with various species of the group and developed a deep interest in becoming better acquainted with the entire genus. Then, in working on a floristic treatment of the caesalpinoid legumes for the *Flora Venezuela*, it was necessary to revise the genus in order to be able to treat the species of *Eperua* authoritatively. Presented herein is a summary of everything I have been able to discover about the group from the field, the herbarium and from the literature.

Numerous persons should be acknowledged as having been helpful to the completion of this monograph, but I especially want to call attention to Nancy Goor, who prepared the drawings, to John Wurdack, who read the manuscript, to Joan Nowicke for her assistance and encouragement with the palynology section, to E. S. Ayensu for his advice in making and interpreting anatomical preparations, and particularly to the Smithsonian Research Foundation, which generously provided grant assistance.

Nomenclatural History of the Genus

As so often happened with Aublet genera, the first two species were described under different

generic names, *Eperua* and *Parivoo*, in widely separated parts of his ground-breaking *Histoire des plantes de la Guiane française* (1775). Even though the greatly elongate, pendent inflorescences and falcate leaflets of *E. falcata* Aublet appear quite dissimilar to the short, erect inflorescences and nonfalcate leaflets of *E. grandiflora* (Aublet) Benth., Schreber (1791) recognized the two species to be congeneric. Following the custom of the time (one of which he was especially observant) he coined a new generic name, *Dimorpha*, to cover the two dissimilar species.

Willdenow (1799) treated both species in his edition of the *Species Plantarum*, providing a new name, *Panzera*, for *Eperua* but retaining Schreber's name *Dimorpha* for the other species. At the same time he added a second species, *D. tomentosa* (Aublet) Willdenow, based on *Parivoo tomentosa* Aublet, which is usually assigned to *Crudia*. De Candolle (1825) was the last of the major encyclopedists to treat this assemblage as two genera, *Eperua* and *Parivoo*, for Benth. and Hooker in their *Genera Plantarum* (1865) combined the two concepts under the one name *Eperua*, admitting only the two original Aublet species. Since then, various authors have described one or two species, mostly in connection with floristic reports—Benth. in the *Flora Brasiliensis* (1870), Miquel in *Stirpes surinamenses selectae* (1850), Sandwith in a review of the genus in Guyana (1931), and Cowan on miscellaneous species in the Guiana Highland (1957 and 1958). Only one attempt at an overall survey of the species has been made—by Ducke in 1940—since Benth.'s review in the *Flora Brasiliensis* (1870).

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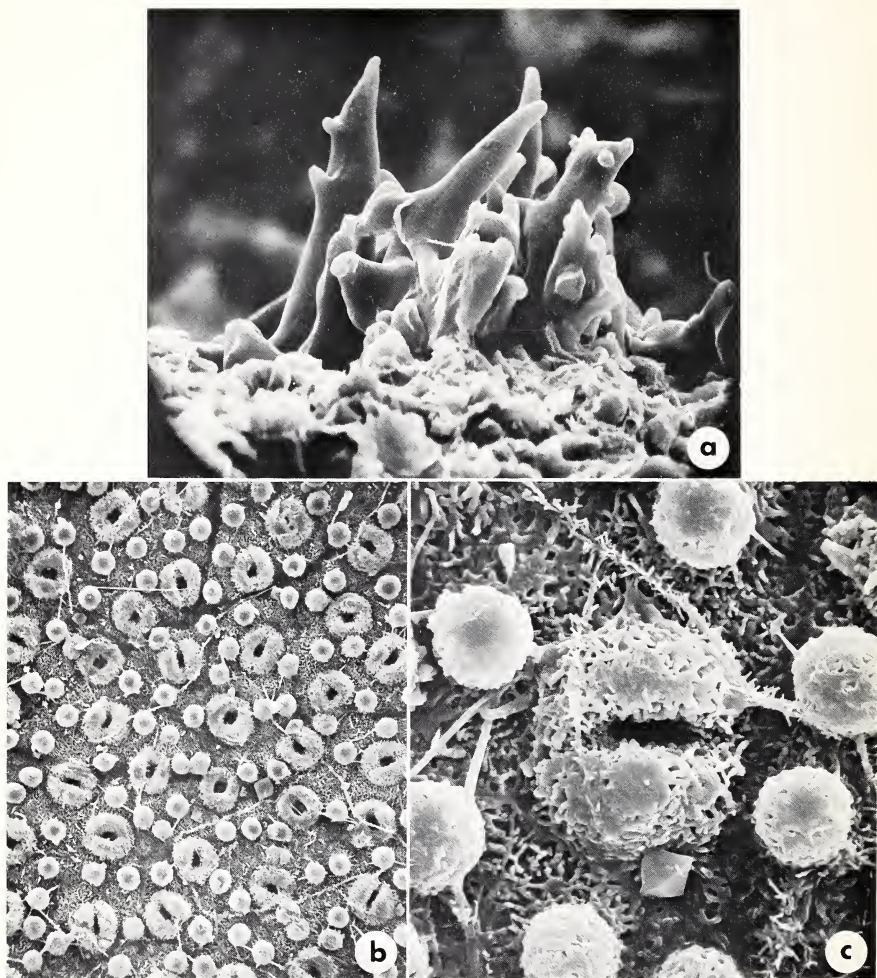


FIGURE 1.—Scanning electron photomicrographs of epidermal morphology: *a*, pubescence of *E. rubiginosa*, $\times 855$; *b*, lower epidermis of *E. purpurea*, $\times 300$ (Maguire 29486, US); *c*, the same, $\times 1500$.

Gross Morphology

Although differing greatly in stature, all the species are trees, some very small (*E. oleifera* var. *campestris*), but others are among the largest in the Amazonian rain forest (*E. purpurea*). The trunks of some of the species are fluted and/or buttressed, but the presence or absence of buttresses may be related to the substrate, rather than being an obligate genetic characteristic. The bark, insofar as there are any data, is smooth except for rather obvious corky lenticels, and gray to brownish-gray or gray-black.

Pubescence is generally simple and microscopic ($\times 15$ or more) to macroscopic but never very long, except on the androecium. In *E. rubiginosa* the hairlets are compound, each one branching irregularly in a dendroid fashion (Figure 1a); those of *E. schomburgkiana* are microscopically bifid, with the appearance of two hairlets arising from the same point.

The stipules are often foliaceous, up to several centimeters long and wide, free from each other, and situated at the two sides of the petiole base. In species characterized by such stipules, however, they may fail to develop completely and then appear as small, inconspicuous "flaps"; thus stipules are less valuable as a source of key characters than would be the case if they were always well expressed. Several species have the stipules partly to completely united laterally into a single bifid or entire body in the leaf axil.

The leaves are uniformly even-pinnate, but the number of pairs of leaflets is not so constant. Four species regularly have only bijugate leaflets (*E. bijuga*, *E. glabriflora*, *E. obtusata*, and *E. venosa*) but most have 3- to 5-jugate ones, sometimes having some of the leaves with only two pairs. There is always a well-developed cylindrical petiole and rachis, as well as obvious petiolules; the blades of the leaflets are usually equilateral and straight, but in three species, all with long, pendant inflorescences, the leaflets are obviously falcate, the two halves of each leaflet consequently more or less unequal. Pubescence on the leaves is rare, but the undersurface of the leaflets in *E. purpurea* is obscured by a microscopic layer of tangled filaments of wax (Figure 1b,c). Venation of the leaflets is generally inconspicuous, sometimes even obscure, but a strong marginal vein is present in *E. pur-*

purea and *E. oleifera* var. *campestris*; sporadically, submarginal veins occur in other species but not so regularly that they provide a means of recognizing the group. The leaflets of most taxa have pellucid punctae, and sometimes they are also present in flower parts, especially in the sepals but never in the petal. In most instances, because of the thickness of the parts, it is necessary to view the leaflets or flower part against a strong light source in order to see the punctae, but in *E. oleifera* and *E. purpurea*, they are more obvious.

The inflorescences are basically the same in all the species, although two species groups can easily be distinguished on inflorescence type alone. Whether elongate-pendent (up to several meters long) or short-erect, a central axis bears a number of racemously disposed lateral branches, each of which is a raceme. Thus, the differences between the two types of inflorescence are essentially the result of one developmental characteristic—the much greater elongation of the peduncle and the axis intervals between branches in the elongate-pendent type. A broad bract, often caducous to deciduous, subtends each flower, the pedicel of which bears, at various levels, a pair of more or less opposite, caducous to persistent bracteoles, very similar in form, size, and pubescence to the bracts.

The cupular hypanthium is somewhat inequilateral in a few taxa (*E. bijuga*, *E. grandiflora*, *E. jenmanii*) but always lined on the inner surface with a palisadelike series of nectaries that project above the rim of the hypanthium or are included within it. Vogel (1968), comparing *Eperua* to *Hymenaea*, considered that each flower has a single nectary which in the former is greatly increased in surface area by radial cleavage or invagination ("radiale Zerklüftung"). My observations lead me to interpret each of Vogel's "folds" as one of several nectaries. In either case, the hypanthium is tightly filled around the gynophore with the nectariferous tissue.

Four strongly imbricate sepals become free from each other at the rim of the hypanthium—they presumably form the outer layer of the hypanthium. Those portions of the outer surface of each sepal, not partially covered by the adjacent ones, bear the pubescence (if any) characteristic of the taxon; the overlapped portions are always glabrous, thinner, often scarious. The sepals are unequal to varying extents in several species, the outer pair, or



FIGURE 2.—Morphology of *Eperua* species. *E. purpurea* (Maguire et al 60112, F): *a*, habit, $\times \frac{1}{2}$; *b*, stipular body, $\times 1$. *E. jenmanii* var. *jenmanii* (Sandwith 710, NY): *c*, foliaceous stipules, ca. $\times 1$. *E. rubiginosa* (Irwin et al 57579, NY): *d*, bud showing terminal extrahypanthial nectaries, ca. $\times 1$. *E. jenmanii* (drawn from plate in protologue): *e*, essential organs. *E. purpurea* (Maguire et al 60112, F): *f*, open, partly dissected flower, $\times 1.5$; *g*, expanded petal, ca. $\times 1$. *E. purpurea* (Ll. Williams 13990, US): *h*, fruit, $\times \frac{1}{2}$.

at least the dorsal one, larger and more strongly concave/cucullate. In three species (*E. glabriflora*, *E. obtusata*, and *E. rubiginosa*) the outer two sepals have a single, large, raised gland near the apex on the outer surface. In *E. rubiginosa* at least these appear to be extrahypanthial nectaries that secrete actively just prior to anthesis (see section on Pollen and Pollination). The sepals vary from green to red to whitish, partly in response to aging of the flowers, and they generally are thickish. The corolla consists of four minute petalodia (up to 10 mm long but usually 0.5–5 mm long) and one large to relatively very large glabrous petal that envelops the essential organs of the flower, producing the appearance of a tubular corolla such as is characteristic of the Bignoniaceae. The range of colors—white, red, purple, lilac, pink, etc.—is also like many of this family, so it is not surprising that there have been family misidentifications by otherwise highly competent field botanists! The width of the petal is often greater than the length so that there is a strong overlap of the lateral margins in bud. In most species the petal is oblate or flabelliform, sometimes tapering obtusely in a claw-like base, but more often the petals are truncate basally. In only one species (*E. venosa*) does the petal bear any pubescence, and in this instance it is only slightly strigulose externally at the extreme base. In bud the petal is strongly crumpled around the infolded stamens and coiled style.

The androecium consists of ten stamens, of which as many as five may be reduced in size and in some species sterile. In most species the smaller anthers appear to produce normal pollen, although its viability is not known. The one dorsal stamen is free from the tube formed by the connation of the other filaments, or it may be briefly joined at the extreme base; it appears to be fertile in all species, but its filament is usually shorter and may be somewhat different in vestiture. The filament tube is equilateral—the union of the filaments to about the same level—or strongly inequilateral by the progressively greater union of the filaments toward the ventral side of the flower (opposite the insertion of the petal). Where there is dimorphism in proportions, the length of the filaments is always greater when they bear the larger anthers characteristic of each species, those bearing smaller or sterile anthers being about the length of the free dorsal one that is invariably fertile. The long-

est pubescence observed in the genus occurs on the filament tube of several species. The anthers are versatile, dorsifixed, oval to narrowly oblong, almost invariably glabrous, and only rarely with apiculate connectives. The thecae are sometimes conspicuously but minutely tessellate and always opening before anthesis.

Within the base of the filament tube the apices of the nectaries are usually clearly evident. According to Vogel (1968), the nectar collects in the space at the base of the petal, but this seems very unlikely in view of the posture of the flower and the adaxial insertion of the petal, unless the nectar is very viscous. On the other hand, it appears entirely reasonable to imagine that the nectar collects within the filament tube, which serves as a reservoir-like structure, ensuring an abundance of pollinator-attracting nectar at anthesis (see section on Pollen and Pollination). If this interpretation is correct, then the deeper, zygomorphic filament tube of some taxa must be a more effective reservoir, at least in more or less horizontally oriented flowers.

The gynoecium is the least variable part of the flower, consisting of an obtuse to capitate stigma, an elongate style (four to ten times the length of the ovary), an oblong-obovate to oblong-oblanccolate ovary, and a short gynophore (generally shorter than the ovary). The stigma is usually entire, but in two species (*E. leucantha* and *E. venosa*) it is somewhat bilobed. The style is always placed at the dorsal margin of the broad ovary apex; that is, the dorsal margin of the ovary continues, scarcely with any change in alignment, as the dorsal surface of the style. The gynophore typically is borne in the center of the regular hypanthium cup but more or less eccentrically in those that are zygomorphic. The ovary contains several ovules.

The fruits are always woody, dehiscent (sometimes violently so in a plant press!), flat (except for dorsal winglike expansions perpendicular to the pod surface in *E. glabriflora* and *E. purpurea*), and more or less oblong to subquadrate. Of those that have the oblong form, several species have falcate, arcuate, or scimitar shapes. One or two oval, flat seeds are found in each fruit; the seed coat is thin-chartaceous and dark colored.

Seedlings of only two species are known certainly, and the first leaves of these have fewer pairs of leaflets than is typical of mature foliage. Seeds

apparently germinate on the surface of the soil, the cotyledons emerge from the testa ("phanerocotyl") sending an elongate epicotyl "canopyward" and an equally elongate primary root into the substrate. The hypocotyl is very short, only a few millimeters long with no special morphology to delimit it precisely.

Epidermal Anatomy

In an effort to clarify further the phylogenetic relationships of the taxa comprising this genus, the anatomy of the epidermis was studied. The technique of applying a liquid plastic to the surface of a leaflet and then observing the resulting "peel" microscopically, failed to yield useful data. Likewise, scanning electron microscope techniques for observing the cellular details were unsuccessful. I am indebted to E. S. Ayensu for his assistance in evolving the following method for rapidly assaying the range of variation in structure of the epidermis of thick, coriaceous tropical leaves.

Small bits of dried leaf tissue roughly 5 mm in length and breadth were placed directly into a mixture of equal parts of 10 percent nitric acid and 10 percent chromic acid and left for at least 24 hours or until the bits became translucent. The samples were then thoroughly washed using a jet of water from a plastic washing bottle. This treat-

ment separates the upper and lower epidermis from the mesophyll, most of which is washed away, but any remaining nonepidermal tissues can be removed with a fine camel-hair brush in a watch glass of water under a dissecting microscope. Small fragments of the epidermis are stained for about five minutes in Toluidine Blue, washed, and then mounted in a water-miscible mountant. The result is only a temporary slide, prepared in a very few minutes, which can be studied at magnifications up to and including oil immersion. If permanent slides are indicated by the preliminary examination, other bits of the cleared sample can be run through conventional stain/dehydration series for mounting in one of the permanent mountants. The Toluidine Blue stain "bleeds" into the temporary mountant, but otherwise slides prepared by this method are usable for at least a few weeks.

In *Eperua* the upper epidermis lacks stomata, so all the data reported below are based on the observations of the lower epidermis. There is more uniformity than anticipated in epidermal characters, for all eighteen taxa showed paracytic-type stomata which, for the most part, are evenly distributed over the surface; in a few taxa, the stomata occur in clusters. (I realize this is a greatly simplified technical description of stomata relative to the ontogenetic terminology proposed by Fyns-Claessens and van Cotthem (1973), but applica-

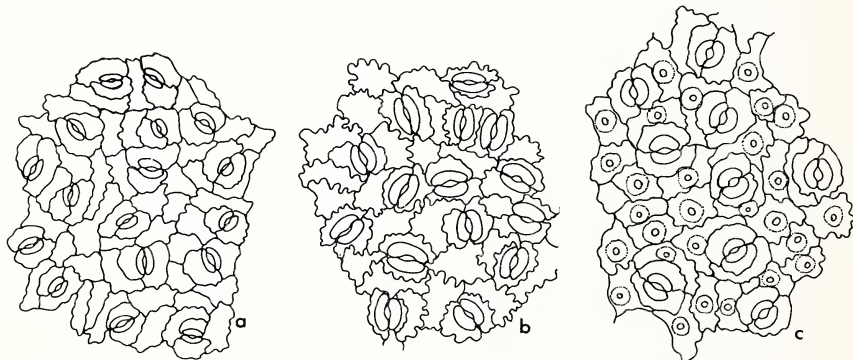


FIGURE 3.—Lower epidermis of species of *Eperua*, $\times 400$: a, *E. oleifera* var. *campestris* (Schultes 10337, US); b, *E. schomburgkiana* (de la Cruz 2172, NY); c, *E. purpurea* (Maguire 29486, US).

tion of this sort of approach to tropical trees is, at least, difficult!) Figure 3a-c indicates the range of variation in size of stomata and of the nonstomatal cells. Also, the extremes of convoluting of the cell walls is illustrated by this figure as well; in other taxa the cell walls are intermediate between these extremes. There appear to be no phylogenetic conclusions to be deduced from epidermal characters in this genus, for there is no correlation with the phylogenetic arrangement suggested by gross morphology and by palynology.

The lower epidermis of *E. purpurea* requires

separate consideration, because it is so different from that of all the other taxa. Figure 1b (SEM, $\times 300$) reveals that the glaucous appearance of the leaflet surfaces is due to a layer of waxlike material, and Figure 1c (SEM, $\times 1500$) demonstrates that the material occurs in the form of branching threads. Doughnut-shaped stomata are easily distinguished from the "ping-pong-ball" shaped bodies which I have referred to as "wax glands." The drawing in Figure 3c indicates that these are produced on ordinary epidermal cells but not on guard cells or subsidiary cells.

TABLE 1.—Summary of pollen data (under "size," figures outside parentheses = range of one-half or more of measurements; figures in parentheses = minimum measurement obtained)

Taxa	Source of pollen	Size	Thickness μm		Aperture	Ektexine morphology
			Sexine	Nexine		
1. <i>E. schomburgkiana</i>	Persaud 166 (US)—Guyana de la Cruz 2172 (NY)—Guyana	(71-)74-78 (74-)78-84*	2-3 1.5-2	0.6-1 1-1.5	3-colporate	punctate-rugulose
3. <i>E. rubiginosa</i> var. <i>rubiginosa</i>	Lanjouw 1209 (US)—Suriname Froes 26649 (US)—Brazil	(82-)91-97 (-101) 78-88*	4-5 4	1.5-2 1-1.5	3-colporate	verrucose
4. <i>E. falcata</i>	Pires 48876 (US)—Brazil Tillett 45791 (NY)—Guyana	(104-)116- 123(-126)* (91-)104- 114(-123)	5-6.5 4-5	1.5 0.7-1.5	3-colporate	reticulate (heterobrochate)
5. <i>E. venosa</i>	Maguire 53597 (US)—Venezuela	(88-)94-104 (-112)	2-2.5	0.7-1	3-porate	punctate-rugulose
6. <i>E. leucantha</i>	Ducke 23289 (US)—Brazil Froes 21104 (NY)—Brazil	(88-)95-101 (-104) (91-)96-104 (-110)	2.5-3 2-2.5	1.5 1-1.5	3-porate	punctate-rugulose
7. <i>E. duckeana</i>	Ducke 244 (NY)—Brazil	(65-)69-71(-75)	2-2.5	1	3-colporate	punctate-rugulose
8. <i>E. glabriflora</i>	Ducke 14A (F)—Brazil INPA 6065 (US)—Brazil	(55-)59-62(-65) (62-)66(-70)*	2-2.5 2.5	1.5 1-1.5	3-colporate	punctate
9. <i>E. bijuga</i>	Ducke 20312 (US)—Brazil Froes 32988 (US)—Brazil	(65-)70-74(-78) (74-)80(-88)*	2-2.5 2.5	1-1.5 1.5	3-colporate	punctate
11. <i>E. grandiflora</i> ssp. <i>grandiflora</i>	Pires 50673 (US)—Brazil Pires 51659 (F)—Brazil	(60-)65-72(-78) (45-)47-53(-60)	2 1.5-2	0.7-1 0.7-1	3-colporate	punctate
12. <i>E. jenmanii</i> ssp. <i>jenmanii</i>	Maguire 33136 (US)—Venezuela Gleason 837 (US)—Guyana	(58-)68-71(-77) (62-)65(-69)*	1.5 1.5-2	1 1-1.5	3-colporate	punctate
13. <i>E. purpurea</i>	Maguire 41922 (US)—Venezuela Prance 15513 (US)—Brazil	65-71(-73) 65-71(-74)	4-5 5	1.5 1.5	3-colporate	reticulate (homobrochate)
14. <i>E. oleifera</i> var. <i>oleifera</i>	Ducke 235a (NY)—Brazil Ducke 213 (NY)—Brazil	48-61(-65)* (51)55-58(-66)*	4-5.5 4.5-5.5	0.7-1 1-1.5	3-colporate	reticulate (homobrochate)

*Based on less than 25 measurements.

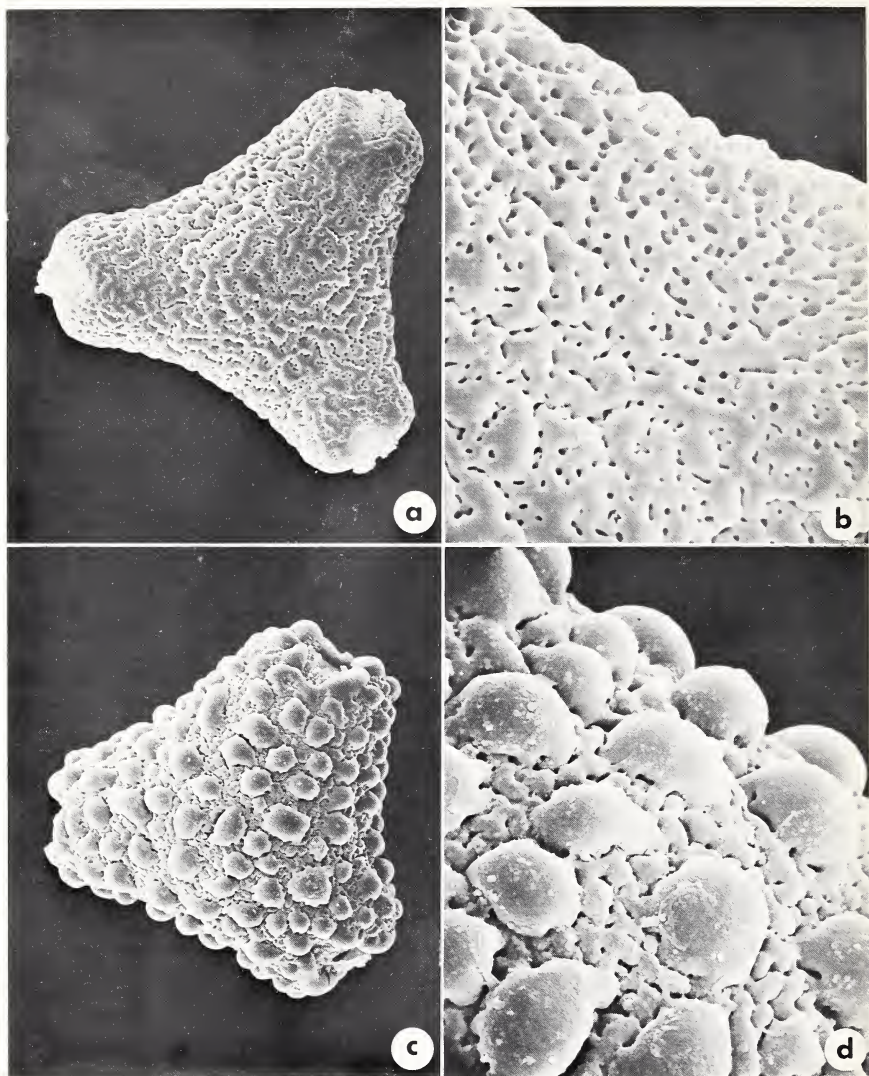


FIGURE 4.—Pollen of *Eperua* species. *E. schomburgkiana* (Persaud 166 US): a, $\times 1000$; b, $\times 3000$.
E. rubiginosa (Lanjouw 1209, US): c, $\times 850$; d, $\times 3000$.

Pollen and Pollination

Anthesis has been observed and detailed in only one species, *E. schomburgkiana*, by Vogel (1968), who described it as a bat-pollinated plant. In this species anthesis begins in early evening, but this may not be true for other taxa, even in those whose flowers are pollinated by bats. In all species the sepals open partially, the bases remain imbricate, and the petal which is strongly crumpled in bud expands. At the same time the infolded filaments reflex and assume the posture characteristic of the taxon involved. In *E. schomburgkiana* a faint odor of crushed leaves ("ein Krautiger Geruch") is evident in the flower at this stage (Vogel, 1968).

Pollen is already released before anthesis, and, at least in some buds, I have observed numerous pollen grains on the stigma which before anthesis is more or less enclosed by the coiled style. The latter characteristic has often been interpreted as an adaptation that at least partially prevents selfing, but differential ripening of the anthers and the stigma is surely a more effective barrier where selfing is deleterious. After anthesis and pollination, all the flower parts except the gynoecium are shed; only in *E. rubiginosa* does the filament tube remain intact around the carpophore of the developing fruit.

There is considerable variation in the form, size, and ornamentation of the pollen grains among the species of this genus; Table 1 is presented in combination with scanning electron micrographs to summarize the variability in a concise way. Observations of overall size and wall thickness were made by light microscopy at $\times 400$, based on 25 or more grains on one or a series of slides made from a single flower. Only grains were measured which appeared to be mature, intact, not damaged by developmental accidents or by preparation of the slides; otherwise the choice of grains to measure was random. Two different collections, often from two distinct geographic locations, were used for each of the twelve species examined. Pollen was not available from two species, *E. glabra* and *E. obtusata*, because of the paucity of material. Fiebender (1959) described the pollen grains of nine of the species, but her observations were limited to those possible with light microscopy, and some of the fine details revealed by the SEM are consequently absent from this important pioneering paper.

Because the grains are flattened equatorially, the material, especially in slide preparations, tends to be oriented in polar view. For this reason, the measurements given in Table 1 represent the height of the triangle, i.e., the distance from any one apex to the base of the triangle. Using this parameter, the grain size ranges from 45 μm to 126 μm . The pollen of one species, *E. falcata*, falls into Erdtman's (1952) "very large spores" class, measuring in excess of 100 μm , three others just short of this size (*E. rubiginosa*, *E. venosa*, and *E. leucantha*), and, in fact, only two samples had grains less than 50 μm . In general, the largest grains are associated with species judged to be advanced sporophytically.

The thickness of the sexine and nexine was measured midway between two apertures and ranges from 1.5 to 6.5 μm for the sexine and 0.7 to 2 μm in the case of the nexine. Although the nexine was of relatively uniform thickness within each grain, the thickness of the sexine was more variable. In some species the sexine thickens near the apertures (*E. glabriflora*, *E. bijuga*, and *E. falcata*). The other taxa have pollen with the sexine equally thick throughout, or it actually thins toward the apertures (*E. schomburgkiana*, *E. venosa*, *E. purpurea*, *E. oleifera*). What significance evolutionarily or biologically to attach to these observations is, at least, uncertain.

COMPREHENSIVE DESCRIPTION OF THE POLLEN.—Grains single, triangular in polar view with an aperture at each angle, flattened equatorially, 3-colporate, rarely 3-porate, the ectexine more or less punctate, punctate-rugulose, verrucose, or reticulate.

Most of the taxa examined (ten of twelve species) had pollen with colporate apertures and the colpi short or reduced, but in two closely related species, *E. venosa* and *E. leucantha* (Figures 5, 6), the apertures are porate and probably represent the ultimate reduction of the colpus. The presence of occasional porate apertures in the "colporate" species appears to reinforce this view. In another species pair, *E. purpurea* and *E. oleifera*, the apertures are distinctive due to the width of the colpus (Figure 9).

Based on morphology, two very general groupings can be recognized—unspecialized pollen and specialized pollen. "Unspecialized pollen grains," 3-colporate with the ectexine punctate or punctate-

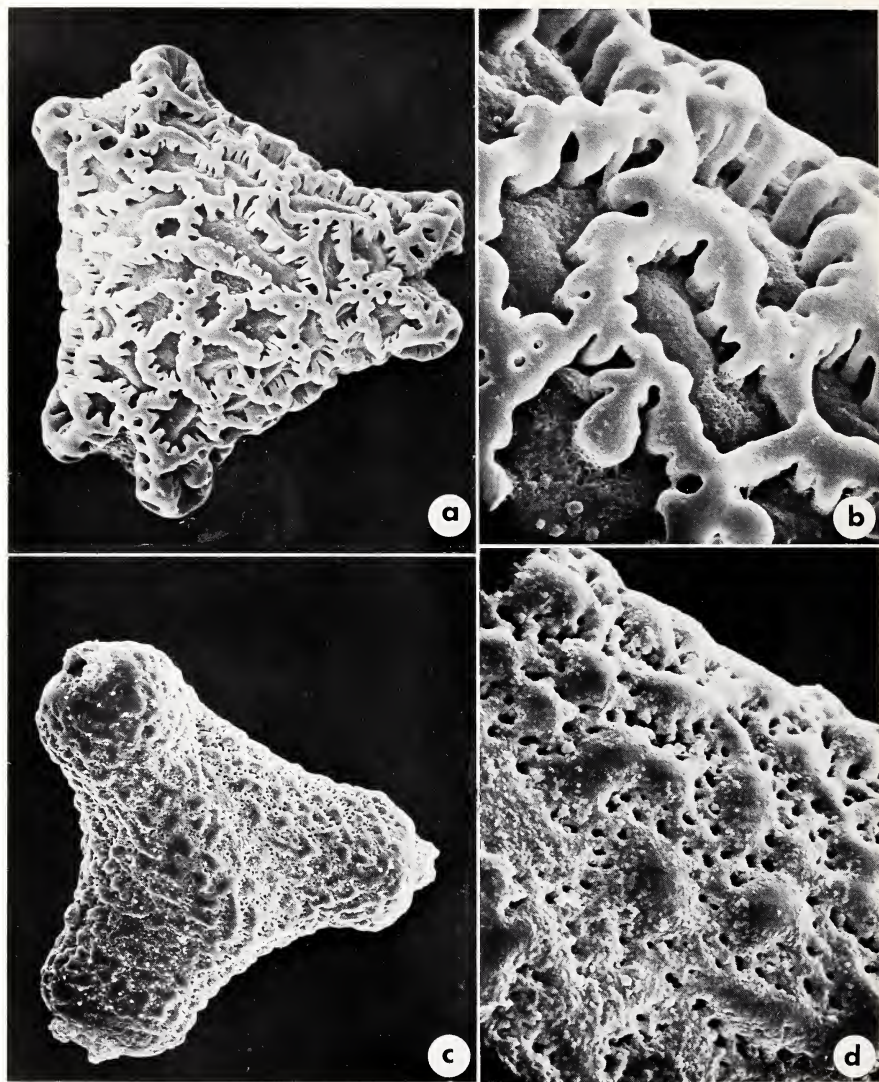


FIGURE 5.—Pollen of *Eperua* species. *E. falcata* (Pires et al 48876, US): a, $\times 850$; b, $\times 3000$.
E. venosa (Maguire et al 53597, US): c, $\times 750$; d, $\times 3000$.

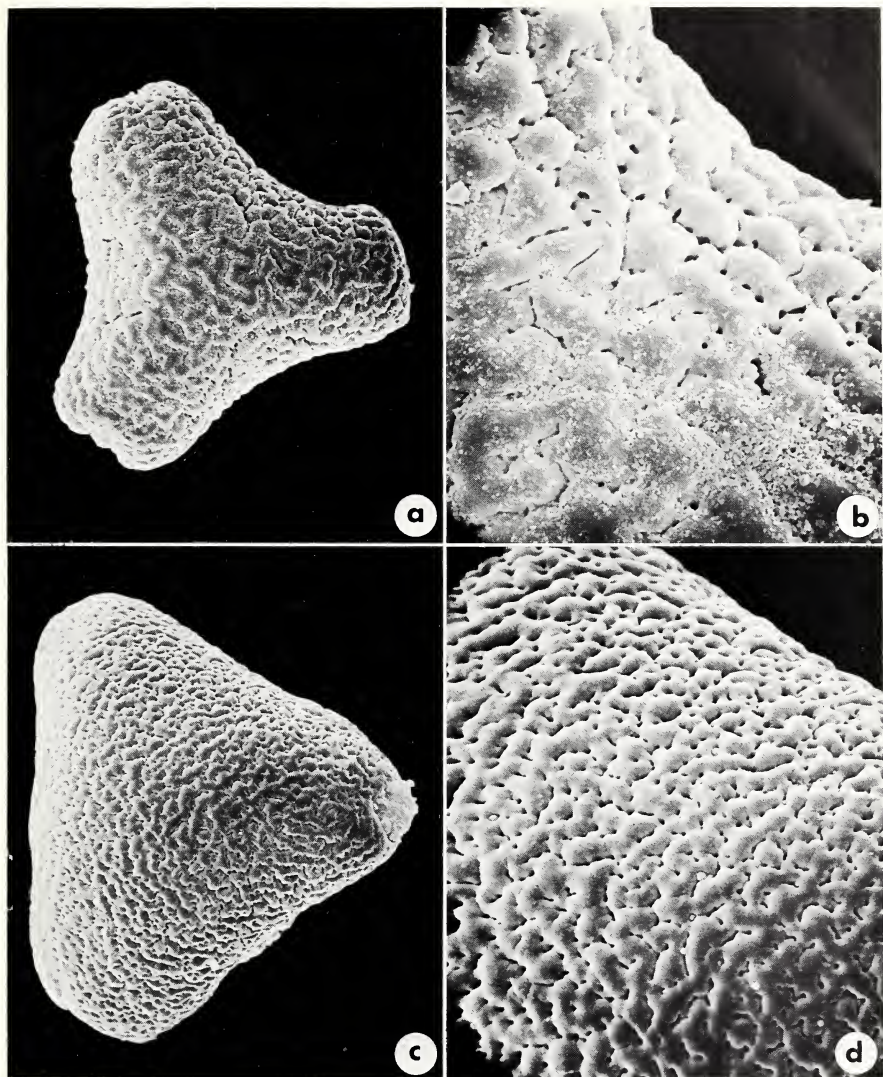


FIGURE 6.—Pollen of *Eperua* species. *E. leucantha* (Ducke 23289, US): a, $\times 850$; b, $\times 1400$.
E. duckeana (Ducke 23734, US): c, $\times 1400$; d, $\times 3000$.

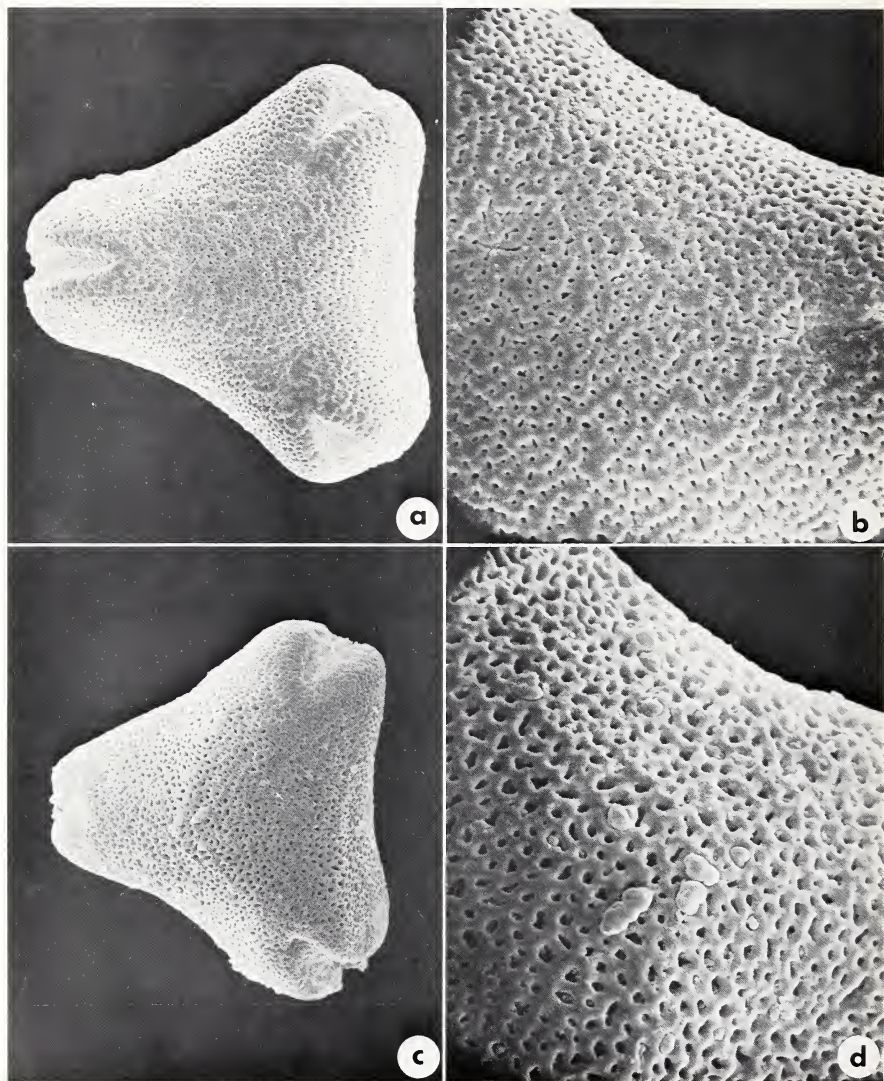


FIGURE 7.—Pollen of *Eperua* species. *E. glabriflora* (Ducke 14a, F): a, $\times 1400$; b, $\times 3000$.
E. bijuga (Ducke 20312, US): c, $\times 1000$; d, $\times 3000$.

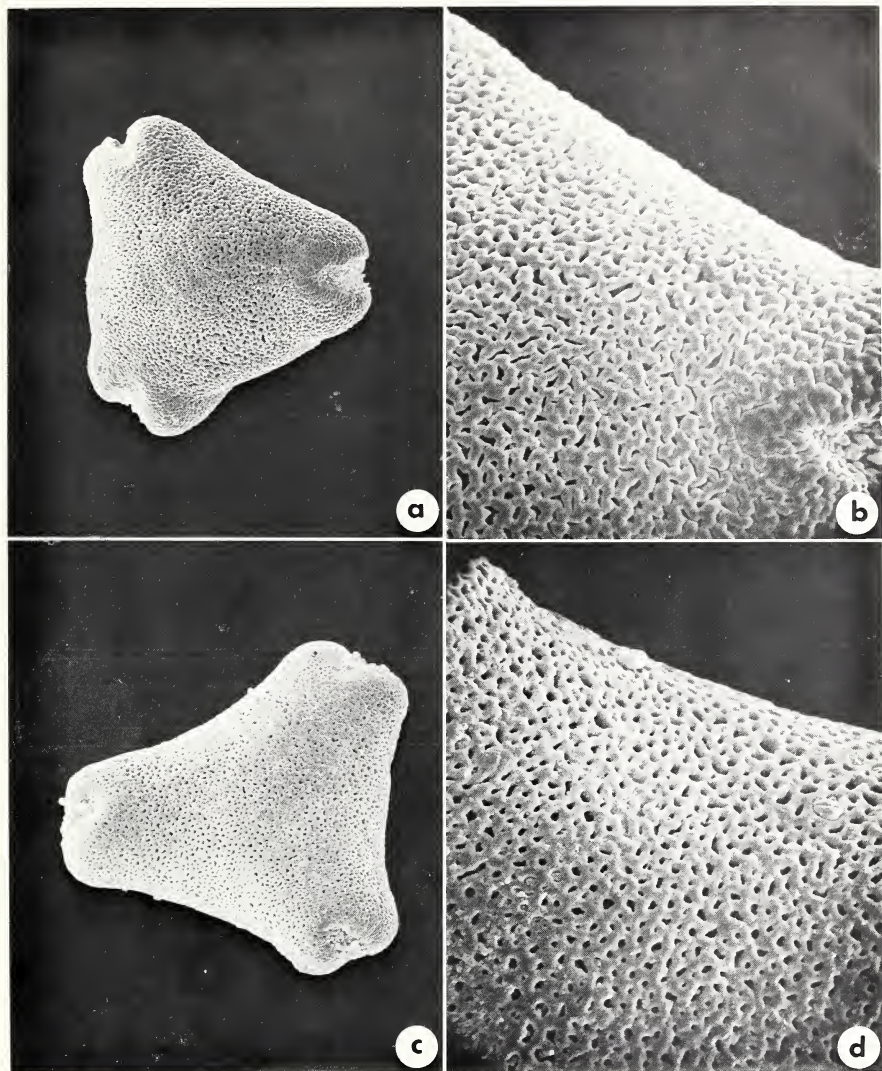


FIGURE 8.—Pollen of *Eperua* species. *E. grandiflora* (Pires 50673, US): a, $\times 1000$; b, $\times 3000$.
E. jenmanii (Maguire 33136, US): c, $\times 1000$; d, $\times 3000$.

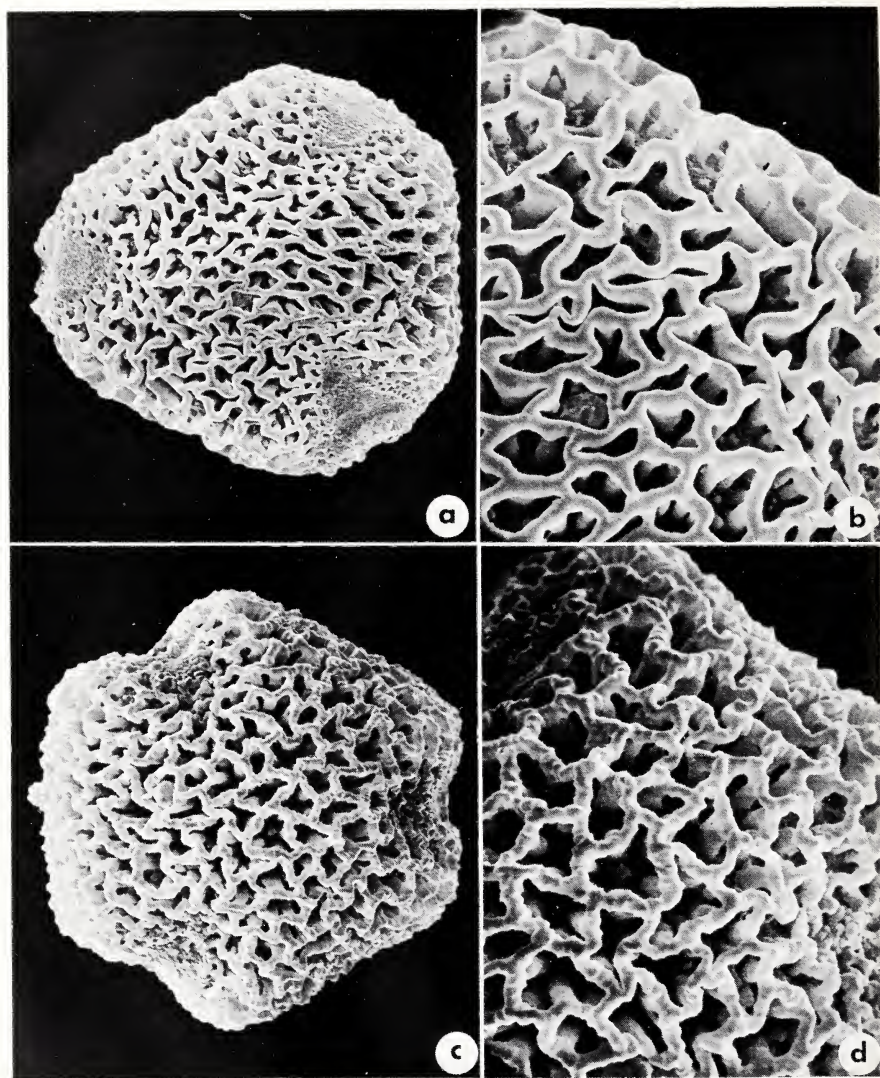


FIGURE 9.—Pollen of *Eperua* species. *E. purpurea* (Maguire 41922, US): a, $\times 1350$; b, $\times 3000$.
E. oleifera (Ducke 235a, NY): c, $\times 1700$; d, $\times 3000$.

rugulose, are found in six species: *E. glabriflora*, *E. bijuga*, *E. jenmanii*, *E. grandiflora*, *E. duckeana*, and *E. schomburgkiana* (Figures 4a,b; 6c,d; 7, 8); the latter two could have been separated by the rugulose character of their ectexine, but the difference is not sharply defined. The category "Specialized pollen grains" includes those types that appear to be derived or advanced in some characteristic: *E. oleifera* and *E. purpurea* (Figure 9) have grains with the ectexine homobrochate-reticulate and, moreover, they have the most prominent colpi; *E. leucantha* and *E. venosa* (Figures 5, 6) are the only taxa with porate apertures, regarded as advanced (see discussion above), but have a relatively unspecialized ectexine; *E. rubiginosa* (Figure 4) has an ectexine that is conspicuously verrucose, a condition that could be derived by an elaboration of the larger elements or folds in a punctate-rugulose ectexine, such as is found in *E. venosa* and *E. leucantha* (Figures 5, 6); the pollen grains of *E. falcata* (Figure 6) are distinctive by virtue of the reticulate ectexine in which, unlike the reticulum of *E. purpurea* and *E. oleifera* pollen, the brochi are of very variable sizes (heterobrochate).

There have been very few observations of the visitors to flowers of any species of *Eperua* and none that give unequivocal evidence of the true pollinators. H. S. Irwin (pers. comm.), however, has observed large black ants and hummingbirds visiting flowers of *E. rubiginosa* during daylight hours, bats at dawn and at dusk. Which of these groups effect pollination is unknown at this time and all may be involved, the ants in selfing, the bats and hummingbirds in outcrossing. In *E. rubiginosa*, however, ants may very well be pollinators; in a photograph generously provided by Irwin of an inflorescence branch, one can clearly see a drop of liquid ("a sticky drop," fide Irwin) at the apex of each bud just before anthesis. This is one of the species with the two outer sepals bearing a single large dorsal "gland" near the apex. I suspect that these are extrahypanthial nectaries that function just before anthesis to "advertise" to potential pollinators the coming attractions of the hypanthial nectar flow. In other words, pollinators would be attracted to the mature buds so that large numbers would be present at anthesis. Since ants are not likely to move from tree to tree of the same taxon, it would seem that ant pollination, if it does occur regularly, is tantamount to

describing the plants as self-compatible. While all this may be true, it is speculation at the moment and needs field checking to verify. At least in some other tropical legumes the same swarms of ants are present in the inflorescences at anthesis, but Mary K. Arroyo (pers. comm.) believes that in these instances the ants serve to protect the tender, often succulent flower parts against predators. This view has also been expressed by Thomas Elias and Howard Irwin at the New York Botanical Garden (pers. comm.). The situation may be exactly the same in *Eperua*, but at this moment there are no published observations to solve the riddle.

One may as well credit as pollinators the bats and hummingbirds that visit the flowers of this and closely related species. The long-exserted stamens, surpassed considerably by the elongate style, appear to provide for the shedding of pollen on the backs of such visitors as they enter the flower in search of nectar. Vogel (1968) considered *E. schomburgkiana*, *E. leucantha*, *E. falcata*, and *E. rubiginosa* to be chiropterophilous, largely because of the morphology of the flower and inflorescence, rather than because he or others had observed bat visitors to the flowers covered with pollen. He pointed out that the following are melittophilous species: *E. bijuga*, *E. purpurea*, *E. jenmanii*, *E. oleifera*, and *E. grandiflora*, but he also apparently reached that conclusion on the basis of morphology, rather than on field observations.

If, in fact, *Eperua* species "cover all their bets" by employing both selfing and outcrossing in accomplishing fertilization, this would seem to have considerable adaptive advantage. Such a situation is of course intermediate between the position taken by Fedorov (1966), Baker (1959), and others (that low density of individuals and asynchronous flowering among tropical trees naturally leads to self-compatibility and selfing) and the views of Bawa (1974), Ashton (1969), and others who hold either that outcrossing is the rule or that it is the more commonly effective breeding system. One of the more rewarding areas for investigation in biology presently is that concerned with these and related phenomena.

Ecology and Phenology

There is always a dearth of ecological data when one is studying tropical plants, especially when one

must rely almost exclusively on collection data. As Brainard once remarked in his work on *Viola* in North America, one suspects that distribution maps reflect more the itineraries of collectors than the range of the plant species they purport to show. In the neotropics, one is faced by this same phenomenon, intensified by the difficulty of reaching much of the region, even now when technology is opening the interior regions to exploration. Add to this the fact that in the rain-forest regions where so many of the tree legumes abound in numbers of species and individuals, there is a several-month-long rainy season that discourages most collectors. So one is left with compiling data from collections made primarily during the drier parts of the year in accessible areas. The following, admittedly incomplete, account is based solely on data from labels on collections, mostly made under these conditions.

Plants of the genus *Eperua* are almost invariably lowland rain forest trees, often along rivers and streams (this latter condition may reflect the fact that most collecting has been done along rivers, the principal transportation routes where roads have not yet penetrated). Some species are best developed in that part of the forest above the influence of annual flooding, while others occupy the regularly flooded portions (especially *E. falcata*). Very often *Eperua* species grow along blackwater streams, and Janzen (1974) in a review of existing data on the cause of such rivers and lakes cites leaching of "humic acids and probably other toxic organic compounds" from *Eperua* leaves, among others. He would also contend that the evergreen leaves of most species is an adaptation to poor soils, too poor to permit replacement of leaves regularly. And many *Eperua* species do occur on white or brown sands in forest or savanna scrub. Two taxa occur in drier, nonforest situations: *E. purpurea* generally is a plant of savanna scrub, and *E. oleifera* var. *campestris* occurs in grassy savannas. Dominance of one *Eperua* species or another is so pronounced in some areas as to approach the kind of forest one finds in temperate zones dominated by one or a few tree species. Janzen concluded that seeds of *Eperua* probably "will be found to be very toxic." This could explain the relatively pure stands of wallaba species—a result of the development of a built-in predator deterrent, perhaps even a biocide, in the seeds. Certainly the large

number of seedlings sometimes seen simultaneously germinating beneath a parent tree suggests at least "unpalatable" seeds. He discarded the possibility of mast-fruiting as a means for the genus to overcome predator destruction. Other factors involved in the evolution of tropical forest were reviewed by Ashton (1969).

Soils in the hylaea are often sandy and in Guyana there is a regular relationship between the kind of soil and the *Eperua* species it supports—white sand and brown sand soils usually have different species. According to Ducke (1940), *E. glabriflora* is found in places with moist acidic soil of white sand and black humus, *E. schomburgkiana* on the marshy banks of small forest rivers and streams.

Altitudinally the range for the genus is not great, all taxa occurring below 1000 m elevation: *E. bijuga* occurs along watercourses at the mouth of the Amazon River, near sea level, and most species occur below 500 m; *Eperua jenmanii* has been collected up to 1000 m and *E. falcata* at 700 m elevation. In this respect, *Eperua* taxa are typical of the vast majority of woody legumes in the neotropics—they are essentially a lowland component, albeit a very critical one in terms of biomass, of the tropical rain forest.

Fanshawe's classic paper on the vegetation of Guyana (1952) is particularly instructive with respect to *Eperua* ecology. Although the area considered there (Guyana) is not typical of all parts of the range of *Eperua*, it is certainly a good representation of much of it. Using Beard's classification of climax vegetation in tropical America (1944), Fanshawe described the components of 28 formations, in at least seven of which one or more species of *Eperua* occurs. Some species are narrowly restricted, and none occur in either his Coastal Zone or his Southern Upland Region, but one species, *E. falcata*, is able to tolerate or to take advantage of a wide range of soil types, water supply, elevation, and to endure man-made or natural disturbances, such as clear felling and burning for shifting agriculture or storm destruction. In most areas, however, it typically forms a nearly pure stand on the floodplain along the rivers. Just above its range, on the land behind the floodplain and above annual flooding, *E. rubiginosa* is dominant (H. S. Irwin, pers. comm.). In the Lowland Region, which stretches from the northwest, southeasterly to the southern uplands, forests of *Eperua* in com-

bination with various other subdominants and associates cover large areas. These occur in two forms principally and on two general soil types: (1) Dry Evergreen Forest on the central white sand penepain or on redistributed white sands derived from it; and (2) in Swamp Forest on alluvial flats alongside rivers. The same sort of pattern prevails in the mountainous sandstone region of the Pakaraima Mountains.

From the incomplete data available it appears that most species flower during the (relatively) dry season at its driest, others at the end of the dry and the beginning of the rainy season; fruits usually mature in the rainy periods. *Eperua bijuga*, however, appears to flower and fruit during the rainy season (April to August); *E. leucantha* and *E. falcata* flower and fruit during the dry season (September to March).

Geography

The species of *Eperua* are unusually restricted for a lowland legume genus. All known species occupy the northeastern quarter of the South American continent from 10° south to the north coast and from about 73° west longitude, east to the Atlantic, boundaries that coincide well with those of the Amazonian Hylaea. Of the eighteen taxa recognized in the genus, only five occur south of the equator and only four are unknown in Venezuela and the Guianas. There are large inexplicable gaps in the distribution where considerable collecting should have turned up one or more taxa. The whole Brazilian mid-Amazon and mid-Rio Negro areas have had relatively good attention by collectors, but the map shows an absence of *Eperua* localities. The vast preponderance of both individuals and kinds occur in the southeastern Colombian-southwestern Venezuela-Guianas Arc. A secondary concentration of taxa occurs in the Manaus area. Collecting in the distribution gaps listed above, as well as in the species-rich lowland forest area of southeastern Colombia may be expected to yield many additional distribution records and very likely undescribed taxa.

Economics

The name "wallaba" is applied to timbers of several species of *Eperua*, the commonest, *E. fal-*

cata, is generally called "soft wallaba." The wood of *E. jenmanii*, usually called "ituri wallaba," is indistinguishable commercially (but is different even to the unaided eye) from soft wallaba (Aitken, 1930). The trees grow rather rapidly and regeneration is relatively rapid, about thirty years from cutting to cutting. Wallaba forest grows naturally on agriculturally useless white sands, which are capable of producing an average of 600 cubic feet of marketable wallaba timber per acre (Aitken, 1930).

The sapwood is dingy white with resinous streaks, but the darker heartwood is decidedly resinous. The heavy, hardwood splits rather cleanly, although the gummy exudate makes working it difficult in the same way as does "fat pine" wood. Although paper-pulp experiments indicate it to be an uneconomical source of pulpwood, the timbers are used widely throughout Guyana for house framing, vat staves, fence poles, telephone poles, and shingles, as well as for firewood and charcoal. It is particularly resistant to decay in contact with water and mud. (During a visit in 1954 I was told that a seaplane ramp, being built of wallaba planks into one of the northern Guyana rivers, should be serviceable for at least 25-30 years, even though submerged!)

Ducke (1940) reports that the two forms of *E. oleifera*, *E. bijuga*, and *E. purpurea* had been in cultivation for four to six years in 1940 in the Jardim Botânico do Rio de Janeiro; *E. falcata* is planted in Trinidad, West Java, and Cameroon; and *E. jenmanii* has been grown in Mexico, Singapore, Cameroon, Jamaica, and Trinidad.

Phylogenetic Speculations

There seems to be little cause to doubt that *Eperua*, *Heterostemon*, *Elizabetha*, and *Paloue* form a close-knit cluster of genera, even though they have been considered (Engler & Prantl, 1894) to be more distantly related by virtue of the fact that the latter three genera, and others, have three to five petals and/or their flower buds are enclosed in enlarged bracteoles before anthesis. But it is even more speculative to suggest where this genus cluster should be associated. Vogel (1968) believed that *Eperua* and *Hymenaea* are closely related, a view shared by Lee and Langenheim (1975) in their monograph of the latter genus. However, I

5. Zygomorphic hypanthium and staminal tube are relatively advanced.

6. Unequal sepals with extrahypanthial nectaries are evidence of advancement.

7. Bilobed stigmas are an elaboration of simple capitate, capitate, or truncate stigmas.

8. Punctate-psilate ectexine is interpreted as less advanced than punctate-rugulose, verrucose, and reticulate, in that order.

9. Colporate pollen apertures preceded porate ones evolutionarily.

Some of these trends are characteristic of the subfamily Caesalpinioideae generally, especially the tendency for reduction in leaflets per leaf, and the progressive sterilization of some members of the androecium. The presence of only a single petal in *Eperua* is only one example of the oft-expressed tendency for reduction in petal number in the subfamily.

As W. H. Wagner has often remarked in discussing his "ground plan" method of representing phylogenies in this graphic form, one of its great strengths is that it forces one to study very intently all the characters of a group, to evaluate them and to judge how they interrelate. In Table 2, only

the most significant characters are included, together with their character-states, for each species. Subspecific taxa are not treated separately in the table because all parts of each species are the same with respect to the characters/characteristics included.

The immediate precursors of extant *Eperua*-species must have had leaves with numerous pairs of leaflets, foliaceous-lateral stipules, erect inflorescences bearing flowers whose sepals were of equal size and form and lacking extrahypanthial nectaries, with a regular cupular hypanthium, a short regular staminal tube bearing ten functional anthers enclosing pollen with punctate ectexine and germinating by means of three colporate apertures on nonbilobed stigmas. The solid circle in Figure 10 represents such an assemblage of unspecialized characteristics, from which the modern species have evolved by acquisition of more advanced traits. *Eperua schomburgkiana*, for example, is advanced beyond the ancestral state principally by its sepals that are unequal in size and form; on the other hand, *E. falcata* is relatively far removed by its accumulation of six character-states which I have interpreted to reflect advancement. The

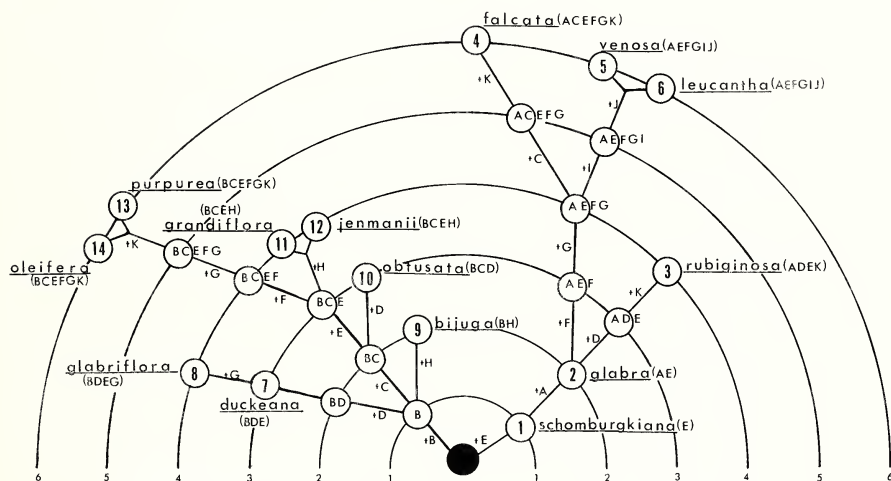


FIGURE 10.—Ground-plan diagram of phylogenetic relationships in *Eperua*.

concentric semicircular lines represent evolutionary stages, each with a progressively larger number of specializations. The capital letters along the radiating lines, as well as those labeling the unnamed hypothetical taxa and in the formulas in parentheses after each specific epithet connote the characters listed in Table 2.

Many speculations can be made on the basis of this diagram at once but these are probably obvious. What would be most interesting would be the discovery in the field, or herbarium, of some of the hypothetical taxa depicted! Such an event would tend to validate what is otherwise highly putative.

Eperua Aublet

Eperua Aublet, Pl. Guian. 1:369, t. 142, 1775.

Parivoo Aublet, Pl. Guian. 2:756, t. 303, 1775.

Dimorpha Schreber, Gen. Pl. 2:493, May 1791.

Pansera Willdenow, Sp. Pl. 2:540, March 1799.

Small to very large trees (5–70 m tall); stipules 2, often free, foliaceous and conspicuous but sometimes joined in a bifid or entire, compound intrapetiolar body; leaves alternate, paripinnate, the

leaflets 2- to 6-jugate, usually glabrous, pellucid-punctate, falcate or straight; inflorescence racemes, usually compound, long and pendent or short and erect, the flower subtended by a small bract at the pedicel base and two bracteoles arising at various levels on the pedicel; flowers pedicellate, the hypanthium cupular, regular to zygomorphic, the inner wall obscured by a palisade of nectar-producing glands; sepals four, equal in size and shape or the dorsal one larger and more concave, the two outer ones sometimes with a single gland near the apex dorsally, strongly imbricate; petal one, usually glabrous, oblate or flabelliform, obconate or truncate basally; stamens 10, all fertile or up to 5 reduced to staminodia, the dorsal one fertile, free or joined at the base with the tube formed by the union of the filaments in their lower part; stigma obtuse to capitate, entire or bilobed, the style filiform, the ovary oblong-oblancheolate to obovate, the gynophore centric to nearly so in the hypanthium; fruits woody, dehiscent, scimitar-shaped to subquadrate, the seeds one to few, oval, flattened laterally.

TYPE-SPECIES.—*Eperua falcata* Aublet, Pl. Guian. 1:369, t. 142, 1775.

Key to the Taxa of *Eperua*

1. Inflorescence long-pendent, to 2.5 m long; ovary usually longer than gynophore 2
 Inflorescences erect or at least not pendent, only a few centimeters long; ovary and gynophore about equal in length 7
2. Leaflets falcate; stipules intrapetiolar, bifid or entire 3
 Leaflets not falcate; stipules free from each other, lateral at the base of the petiole 5
3. Leaflets mostly bijugate and 14.5–22 cm long, 8–9 cm wide, the base regularly inequilateral, the venation prominent; petal very shortly unguiculate, sericeous externally at the base 5. *E. venosa*
 Leaflets mostly 3-jugate, not as in the preceding; petal truncate basally, sessile, glabrous 4
4. Petal white, 25–30 mm long, 40–50 mm wide; buds with a gray bloom (minutely puberulous); inflorescences 6–9 dm long, the axis minutely puberulous, the axis of the lateral branches mostly 10–15 mm long at anthesis; staminal tube strigose-sericeous; fruits minutely strigulose 6. *E. leucantha*
 Petal pink to scarlet, 13–18 mm long and 19–25 mm wide; buds brownish-strigulose; inflorescences 10–14 cm long, the axis somewhat microstrigulose, the axis of the lateral branches about 30–50 mm long or even longer at anthesis; staminal tube villous; fruits more or less minutely puberulous 4. *E. falcata*
5. Plant with many parts minutely tomentulose, the hairs multicellular, irregularly branching, rusty-colored (at least $\times 60$), petal dark pink to red or purple-red, 13–20 mm long, 22–35 mm wide; filaments 35–55 mm long, the anthers 5.5–7 mm long (3. *E. rubiginosa*) 6
 Plant glabrous in all its parts; petal cream-colored, 28–30 mm long, 35–50 mm wide; filaments about 78 mm long, the anthers 9 mm long 2. *E. glabra*
6. Leaf rachis usually 12.5 cm long or shorter, the leaflets 3-jugate; sepals 13–20 mm long, 4–9 mm wide 3. *E. rubiginosa* var. *rubiginosa*
 Leaf rachis usually more than 15 cm long, the leaflets 4- or 5-jugate; sepals 21–35 mm long, 7–15 mm wide 3b. *E. rubiginosa* var. *grandiflora*

7. Leaflets bijugate 8
- Leaflets 3- to 6-jugate 10
8. Apex of leaflets rounded-obtuse, partly retuse 10. *E. obtusata*
- Apex of leaflets acute to acuminate 9
9. Leaflets narrowly revolute marginally; inflorescence axes glabrous; bracteoles 9–10 mm long, oval-ovate; pedicels and sepals glabrous; northwestern Brazil 8. *E. glabriflora*
- Leaflets plane; inflorescence axes puberulous; bracteoles 5 mm long, oblate; pedicels and sepals puberulous; Lower Amazon Valley, especially near mouth of Amazon River, and in French Guiana 9. *E. bijuga*
10. Leaflet surfaces strongly discolorous, densely papillate-ceriferous on the undersurfaces (at least $\times 30$), the "wax bodies" contiguous, obscuring epidermis; bracteoles obviously scarious marginally, persistent at least to anthesis, triangular-ovate 13. *E. purpurea*
- Leaflets never ceriferous; bracteoles not as above 11
11. Petal white; fruits more or less oblong, more than twice as long as wide 12
- Petal pink, lilac, rose-purple, or purple; fruits more or less quadrate, less than twice as long as wide 13
12. Leaflets mostly 5- or 6-jugate; sepals 22–30 mm long; petal 25–35 mm long, 35–60 mm wide; gynoeceum glabrous; staminal tube equilateral, 10–15 mm long; Guyana and Suriname 1. *E. schomburgkiana*
- Leaflets mostly 4-jugate; sepals 12–18 mm long; petal 14–25 mm long, 22–35 mm wide; ovary and gynophore tomentulose densely; staminal tube somewhat zygomorphic, 3.5–9 mm long; vicinity of Manaus, Brazil 7. *E. duckeana*
13. Petal dark lavender to purple with darker purple and white markings, mottled, basally white, 5–10 cm long and 4–8.5 cm wide (12. *E. jenmanii*) 14
- Petal pink to purple, 2.5–4 cm long and 2.5–5 cm wide 15
14. Bracts, bracteoles, inflorescence axes, pedicels, and hypanthium minutely puberulous; bracts 4–5 mm long 12a. *E. jenmanii* ssp. *jenmanii*
- Bracts and bracteoles glabrous except somewhat ciliate; inflorescence axes, pedicels, and hypanthium glabrous; bracts 2–3 mm long 12b. *E. jenmanii* ssp. *sandwithii*
15. Petal lilac to purple; branchlets, petioles and rachis microscopically pubescent sparingly; hypanthium equilateral; staminal tube villose; southern Amazon Basin (14. *E. oleifera*) 16
- Petal pink; branchlets, petioles, and rachis glabrous; hypanthium inequilateral; staminal tube puberulous; northeast Brazil and Guyana 17
16. Large forest tree with oval to elliptic leaflets, the base rounded-obtuse; petal pale lilac 14a. *E. oleifera* var. *oleifera*
- Small savanna tree with ovate, cordate leaflets; petal rose-purple or purple 14b. *E. oleifera* var. *canpestris*
17. Leaflets minutely venulose, the margins revolute; anthers more or less minutely puberulous; ovary and gynophore densely pilosulose; central to south-central Guyana 11a. *E. grandiflora* ssp. *guyensis*
- Leaflets plane, the venation subobscure; anthers and gynoeceum glabrous; northeast Brazil, coastal French Guiana and southern Suriname 11b. *E. grandiflora* ssp. *grandiflora*

1. *Eperua schomburgkiana* Benth

FIGURES 4, 11

Eperua schomburgkiana Benth, Fl. Bras. 15 (2):226, 1870.

Large shrub or tree 5–36 m tall, the branchlets glabrous, nitid, the stipules 15–43 mm long, 8–22 mm wide, foliose, venulose, coriaceous, deciduous, inequilaterally arcuate-ovate, acute; petioles (13–) 18–25 (–30) mm long, glabrous, the rachis 13–27 cm long, glabrous; leaflets 5- or 6-jugate, the petioles 6–10 (–12) mm long, glabrous, the blades

sometimes irregularly pellucid-punctate, coriaceous to rigid-coriaceous, plane, glabrous, often nitid, (4.5–)7–12 (–15) cm long, (2.5–)3.5–5.5 cm wide, all lanceolate or the basal one or two pairs lanceolate with the other pairs elliptic, the base of the lower one to four pairs obtuse to subobtusate, the base of the upper pairs acute, the apex acuminate to long-acuminate, often mucronulate, the venation more or less prominulous; inflorescence a terminal raceme of racemes 5–14 cm long, the lateral ones in same plane, the axes tomentose, the hairs rusty colored and at least some bifid minutely, the

bracts and bracteoles caducous, sometimes deciduous, 4.5–5.5 mm long and 4–5 mm wide, broadly ovate or oval, concave, tomentose externally; pedicels 11–27 (–35) mm long, tomentose, the hypanthium cupular 4–7 mm long, 5–10 mm in diameter, tomentulose externally, the nectaries projecting above the hypanthial rim; sepals 22–30 mm long, 6–15 mm wide, elliptic to oblong-elliptic, tomentulose externally, the two outer ones larger, concave; petal white, glabrous, oblate to oblate-obovate, 25–37 mm long, 35–60 mm wide; all stamens apparently fertile, the filaments 45–60 mm long, 9 united in an equilateral tube 10–15 mm long, the tube more or less pilosulose or tomentulose, the anthers oval, glabrous, 4.0–5.5 mm long, 1.5–2.5 mm wide; gynoecium glabrous or nearly so, the stigma capitate, the style 45 mm long, the ovary 11–15 mm long, 3.5–5 mm wide, rarely a few hairlets on the dorsal margin near the base, oblanceolate, more or less arcuate, the gynophore 9–17 mm long, glabrous; fruits oblong-oblancoale, 25 cm long, 8 cm wide, somewhat nitid, glabrous, the carpophore 2 cm long, glabrous; mature seeds not seen.

TYPE COLLECTION.—*Robt. Schomburgk 517* (lectotype K, isolecotypes BM, G, K, P, W), "Essequibo & Rupununy. British Guiana, 1838."

DISTRIBUTION.—Riverine forest on sandy soils in northern Guyana and in adjacent Suriname. Flowering June to October.

GUYANA: Above Arrawarri mouth, west bank of lower Essequibo R., 20 March 1909, *Anderson 182* (K, RB); Mazaruni R., no date, *Appun 359* (K); upper Mazaruni R., 22 Sept–6 Oct 1922, *de la Cruz 2091* (F, GH, NY, US), 2172 (F, GH, NY, US); Mazaruni Station, 10 March 1934, *Davis 394* (FD 2390) (K), 7 March 1941, *Fanshawe 644* (FD 3380) (K, NY); Tumatumari, Potaro R., 4–6 July 1921, *Gleason 332* (GH, NY, US), 394 (NY) and 412 (NY); Penal Settlement, 3–9 Dec 1919, *Hitchcock 17089* (GH, US); Mazaruni R., Sept 1880, *Jenman 627* (K), June 1889, 5257 (BM, K, NY); Essequibo R., Sept–Oct 1881, *Jenman 1336* (K); no locality, June 1924, *Persaud 14* (F, NY); Seeba, Oct 1924, *Persaud 166* (F, NY, US); Essequibo R., Moraballi Creek near Bartica, 28 Aug 1929, *Sandwith 142* (K, NY, RB, U, US); mouth of Moraballi Creek, Essequibo R., 11 Aug 1960, *Watson 58* (BM). SURINAME: Corantijn, near mouth of New River, 1 Sept 1935, *Rombouts 170* (NY, U); Wanatoba Falls, Corantijn R., 26 June 1956, *Schulz 7708* (NY, U, US); Corantijn R., 25 July 1950, *Suriname Forestry Bureau 806* (K, U). One collection from Brazil [Pará, west bank of Rio Pacajá, 15 Oct 1965, *Prance et al 1652* (F, NY, U, US)] is in fruit and, ex-

cept for its origin far out of the geographic limits of the species, represents it rather well.

LOCAL NAMES AND USES.—Ituri wallaba (Persaud 166); mahaica-bally (Persaud 14); water wallaba (Persaud 166, Schulz 7708).

DISCUSSION.—Although not very much less advanced than some of the related species, *E. schomburgkiana* combines features (foliaceous lateral stipules, relatively large number of leaflets, erect inflorescences, regular hypanthium and staminal tube, and ten fertile stamens) that seem to locate it near the base of a putative phylogenetic scheme. It is most nearly related, in any interpretation, to *E. dukeana* which was identified by Ducke as a "local form" of *E. schomburgkiana*. The present species differs in having more pairs of leaflets, larger flowers, and a glabrous ovary, as well as in its distribution. Palynologically, the two species are quite similar, the punctate-rugulose ectexine persisting through this evolutionary line to such advanced forms as *E. leucantha* and *E. venosa*, which have long-pendent inflorescences and 3-porate pollen, rather than the short-erect inflorescences and 3-colporate pollen of this basic stock.

This species seems a logical candidate for the taxon from which those species with long-pendent inflorescences may have evolved. Of these, *E. rubiginosa* may be the least advanced; *E. obtusata* is possibly derived from the same stock, for at least both taxa have a conspicuous dorsal gland near the apex of each of the outer two sepals, but *E. obtusata* has short, erect inflorescences and other relatively less advanced characteristics which relate it closely to *E. schomburgkiana*.

2. *Eperua glabra* Cowan

FIGURE 11

Eperua glabra Cowan, Brittonia 8:251, 9 Jan 1957.

Tree 5–20 m tall and to 30 cm in diameter, the bark variegated colored, conspicuously corky-lenticillate, the branchlets glabrous, nitid; stipules caducous, foliaceous, falcate-lanceolate, glabrous, about 2.5 cm long and 1.5 cm wide; leaves glabrous, the petioles (10–)25–35 mm long, the rachis 11.5–19 cm long; leaflets 3- or 4-jugate, the petiolules 5–8 mm long, the blades epunctate, chartaceous,

the lowest pair ovate, cordulate basally, 9.5–14.5 cm long, 5–7 cm wide, those of the other pairs elliptic, 11–17 cm long, 5–7.5 cm wide, the second pair obtuse basally, the upper two pairs acute at the base, all leaflets long-acuminate abruptly, the upper and lower surfaces of the leaflets strongly discolorous, the costa plane above, salient beneath, the venules minutely prominulous; inflorescence a pendent, terminal raceme of racemes to 3 m long, the lateral axes (2–)5–6 cm long, the axes glabrous, the bracts and bracteoles deciduous, glabrous except ciliate marginally, about 2–3 mm long and wide, broadly ovate, the bracteoles arising near the pedicel base; flowers glabrous, the pedicels about 25 mm long, the hypanthium 5 mm long, funnel-form, the nectaries included within the hypanthial cup; sepals 20–22.5 mm long, 8–12.5 mm wide, elliptic, acute, two outer ones cucullate; petal glabrous, 28–30 mm long, 35–50 mm wide, flabelliform, truncate basally, mostly cream-colored but greenish at the base and rose-colored marginally, the petalodia ca. 1.2 mm long, oval, obtuse, glabrous; androecium glabrous, the staminal tube subequilateral, 2.5–3.5 mm long, all stamens fertile, the filaments ca. 78 mm long, the anthers 9 mm long, 2 mm wide, narrowly oblong; gynoecium glabrous, the stigma capitate, the style 60 mm long, the ovary 12.5 mm long, 3.5 mm wide, oblanceolate-oblong, 5-ovulate, the gynophore 8.5 mm long; immature fruit narrowly oblance-oblong, 22–30 cm long, 5–9.5 cm wide, arcuate, the carpophores 3.5–4 cm long.

TYPE COLLECTION.—N.G.L. Guppy 430 (FD No. 7445) (holotype NY, isotypes K, NY, US), near Chodikar Landing, Acarai Mts., 250 m elevation, Guyana, 17 October 1952.

DISTRIBUTION.—Known only from the type locality, the mountainous frontier separating Guyana and Brazil, where it is locally abundant.

GUYANA: Shodikar Creek, 8–22 Jan 1938, A. C. Smith 2882 (A, F, G, NY, U, US).

DISCUSSION.—The closest relative of *E. glabra* appears to be *E. rubiginosa*, which it resembles in inflorescence morphology, lateral stipules, non-falcate leaflets, and in having all ten stamens fertile. It differs in being glabrous in most parts, petal color (cream-colored) and size, stamen dimensions, and in its eglandular sepals.

3. *Eperua rubiginosa* Miquel

FIGURES 4, 11

Eperua rubiginosa Miquel, Stirp. Sur. Select 12, 1850.

Small to medium-sized tree (infrequently larger) 5–20 (–30) m tall, the trunk 12–35 (–90) cm in diameter, the bark brownish-gray, papillate-lenticellate, the branchlets glabrous, often nitid; stipules glabrous, deciduous to persistent, triangular to ovate-triangular, 1.5–3 mm long, 1.5–3.5 mm wide, or foliaceous, venulose, broadly oval, 20 mm long and 17 mm wide; leaves glabrous, the petioles 8–20 (–30) mm long, the rachis 5.5–22.5 cm long; leaflets 3- to 5-jugate (seedlings 2-jugate), the petioles 4–7 (–9) mm long, the blades epunctate, coriaceous to rigidly thick-coriaceous, the margins plane to narrowly revolute, 6.5–13 (–23) cm long, (3–)4.5–6 (–10.5) cm wide, all elliptic or more commonly the basal pair ovate to lanceolate, the base equilateral, obtuse to rounded-obtuse or the second and third pairs subobtuse to acute, sometimes attenuate, the apex acute to long-acuminate, mucronulate to mucronate, the venules subobscure to subprominulous; inflorescence a pendent, terminal raceme of racemes 100–200 (–250) cm long, the lateral racemes (2.5–)4–8 (–16) cm long, the axes microtomentulose, the hairlets multicellular, irregularly branching, rusty colored, the bracts and bracteoles caducous, microtomentulose densely externally, sparingly so on inner surfaces, the bracts ca. 2 mm long and 1.5 mm wide, the bracteoles 2.5 mm long, 3 mm wide, oval-ovate or oblong-oval, concave, arising about one-third of the length of the pedicel from its base; pedicels 20–30 mm long, 1–3 mm in diameter, rusty tomentulose minutely, the hypanthium 3.5–5 (–10) mm long, 4.5–6 mm in diameter, microtomentulose externally; sepals green, the two outer ones larger, cucullate and with one raised gland externally near the tip, microtomentulose externally, glabrous on the inner surface, narrowly oblong to oblong-elliptic to oval, fleshy, 13–30 mm long, 4–15 mm wide; petal glabrous, dark pink to red to purple-red, 13–35 mm long, 22–50 mm wide, broadly oblate to flabelliform, truncate basally, the four petalodia 0.6–1.2 mm long, triangular-ovate, glabrous; stamens persistent with young fruits, most or all apparently fertile, 9 or 10 united basally in an equilateral tube 1.5–3 mm long, glabrous except in the tube

sinuses, 35–70 mm long, the dorsal one shorter, united with the tube at the extreme base or even higher, the anthers narrowly oblong, brown, 5.5–11 mm long, 1.5–2 mm wide, glabrous; stigma capitate, the style 20–80 mm long, glabrous, the ovary 7.5–10 mm long, 2.5–3.5 mm wide, oblanceolate-oblong, truncate apically, densely tomentulose, the gynophore 6–12 mm long, tomentulose minutely; mature fruits to 52 cm long and 12.5 cm wide, oblanceolate, more or less scimitar-formed, arcuate, rusty tomentulose.

3a. *Eperua rubiginosa* Miquel var. *rubiginosa*

FIGURES 2d, 11

Stipules triangular to ovate-triangular, 1.5–3 mm long; leaf rachis 5.5–12.5 cm long, the leaflets 3- or 4-jugate; inflorescences 10–25 dm long, the pedicels about 2 mm or less in diameter just above the bracteoles; sepals 13–20 mm long, 4–9 mm wide.

TYPE COLLECTION.—F. W. Hostmann 229 (lectotype U, isoelectotype K), Suriname R., Suriname. Choice of lectotype is necessitated by Miquel's citation of two syntypes, and this collection was referred to as the type by Amshoff in the *Flora of Suriname*.

DISTRIBUTION.—Frequent to common riverine tree, usually above the level of annual flooding in central Guyana and Suriname on alluvial deposits, coastal French Guiana and northeastern Brazil (Amapá). Flowering from July through November; fruiting August to October.

GUYANA: Arawari Creek, Essequibo R., 22 March 1909, Anderson 183 (K); Essequibo and Mazaruni R., Appun 294 (K); Mazaruni Station, 19 Nov 1934, Davis 404 (FD 2400) (K); no specific locality or date, Fanshawe 2104 (NY, U, US); swamp forest behind Mission, 22 Sept 1952, Guppy 198 (FD 7174) (K, NY, U); Kurupukari, Essequibo R., 27 July 1920, Hohenkerk 122-B (K); Mazaruni R., Sept 1880, Jenman 768 (K) and 786 (K); Essequibo R., Sept–Oct 1881, Jenman 1147 (K); southwest of Bartica, 3 Dec 1923, Linder 132 (GH, NY); Kassikaityu R., upper Essequibo R., 19 Nov 1935, Myers 5672 (K); no locality or date, Robt. Schomburgk 515 (BM, F, G, GH, K, NY, W), Rich, Schomburgk 173 (BM), 174 (BM, G, K, P), and 181 (P); near mouth of Onoro Creek on Essequibo R., 15–24 Dec 1937, A. C. Smith 2741 (A, F, G, NY, U, US). SURINAME: Onobissi, Coppename R., 6 Nov 1916, Gonggrijp 2577 (U); Trakockakreek, 21 Oct 1921, Gonggrijp 5515 (U); Kayser Airstrip, 45 km above junction of Zuid R. with the Lucie R., 25 Sept 1963, Irwin et al 57579 (M, NY, U, US); Suriname R., Oct 1844, Kappler 1689 (syntype of *E. rubiginosa*

Miquel) (G, P, U, W); Arakuckakreek, Kegel 872 (NY) Coppename R., near Ralegh Falls, 10 Sept 1933, Lanjouw 738 (U); Suriname R., near Kabelstation, 10 Nov 1933, Lanjouw 1209 (U, US); bank of Marowijn R., south of Albina, 19 Sept 1948, Lanjouw & Lindeman 324 (K, NY, U); Coppename R., near mouth of Wuyombo R., 23 July 1954, Lindeman 6344 (U); near junction of Zuid and Lucie Rivers, 7 July 1963, Maguire et al 54014 (F, G, GH, NY, RB, U, US); Raleghvallen, Coppename R., 24 Sept 1954, Menega 102 (U); Corantijn R., near junction with New R., 1 Sept 1935, Rombouts 177 (U); Litanie R., Aug 1937, Rombouts 725 (BR, U); no locality, Suriname Forestry Bureau 311 (K, U); Biegie Stong, 18 Sept 1949, Suriname Forestry Bureau 603 (K, U); Coppename R., 17 May 1950, Suriname Forestry Bureau 704 (U); upper Suriname R., 16 June 1921, Suriname Forestry Bureau 5462 (U); Suriname R., 10 July 1908, Tresling 96 (U), 102 (U), near Goddo, 19 Aug 1908, 334 (RB, U); Gonini R., Aug 1903, Versteeg 157 (U); Tapanahoni R., Aug 1904, Versteeg 855 (U); no locality or date, Voltz s.n. (U); lower Coppename R., Aug 1901, Iwent 116 (U); Para, 1852, Wullschlägel 149-A (BR); Jodensavanna, upper Suriname R., 1852, Wullschlägel 150 (BR), 2069 (W). FRENCH GUIANA: Comté R., Belizón, Apr 1961, Aubreville 313 (P); Balaté Creek, 23 Sept 1954, BAFOG 219M (P, U); Crique Ouauqui, Grand & Petite, 7–13 Sept 1961, BAFOG 7831 (U); Itany and Marouini, 29 Sept–2 Oct 1961, BAFOG 7937 (U); Saut des Polissoirs, Lunier R., 1897–98, Geay s.n. (P); Saut Grand Bacon, Mana R., Halle 732 (P, US); Rio Oiapoque, across from Colonia Agricola do Oiapoque, 4 km north of Cricu River, 13 Aug 1960, Irwin et al 47471 (NY, U, US); no locality, 1792, Leblond s.n. (G, P); no locality or date, Leprieux s.n. (G, P, US); no locality or date, Martin s.n. (BM), Melmon 102 (P); no locality, 1821, Perrotet 23 (G); no locality or date, Perrotet s.n. (P), Poiteau s.n. (G, K); no locality, 1863, Rech 45 (P); no locality, 20 Oct 1938, Vaillant s.n. (P). BRAZIL: Pará: Rio Mapuera, 3 Dec 1907, Ducke 9022 (G, RB); Coumany, 22 Oct 1895, Goeldi 1158 (BM, G, RB, US). Terr. do Amapá: Oiapoque R., 1 Oct 1949, Black 49–8301 (GH, INPA, NY); Oiapoque, Rio Oiapoque, Black et al 54–17621 (IAN); Parque Indígena do Tumucumaque, Rio Pará de Oeste, Missão Tiriyo, 27 Feb 1970, Cahalante 2538 (NY); Rio Oiapoque, Aug 1949, Candido s.n. (IAN); Rio Oiapoque, 29 Jan 1950, Froes 25698 (IAN) and 15–16 Oct 1950, Froes 26638 (IAN, US), 26639 (US), 26649 (IAN, RB, US); no exact locality or date, Luetzelburg 20211 (M, W); Oyapock, Salto Guamá, July 1927, Luetzelburg 20399 (M); Rio Oiapoque near base of granite outcrop near Mt. Carupina, 15 Oct 1960, Pires & Westra 48849 (F, NY, US); Rio Araquari between Monguba and Serra do Navio, 25 Sept–4 Oct 1961, Pires et al 51182 (NY, U, US), 51501 (NY, US); Valle da Serra Tumuc-Humac, 3 Dec 1928, Sampaio 5760 (R); Pará do Cuminiá, 7 Dec 1928, Sampaio 5818 (R).

LOCAL NAMES AND USES.—Apa (Irwin & Westra 47471), oeverwallaba (Maguire et al 54014), ouapa (Halle 732), walaba (Lanjouw 1209), wapa rouge (Lemee s.n.), watafa (Guppy 198).

3b. *Eperua rubiginosa* Miquel
var. *grandiflora* Pulle

FIGURE 11

Eperua rubiginosa Miquel var. *grandiflora* Pulle, Enum. Vasc. Pls. Surinam 211, 1906.

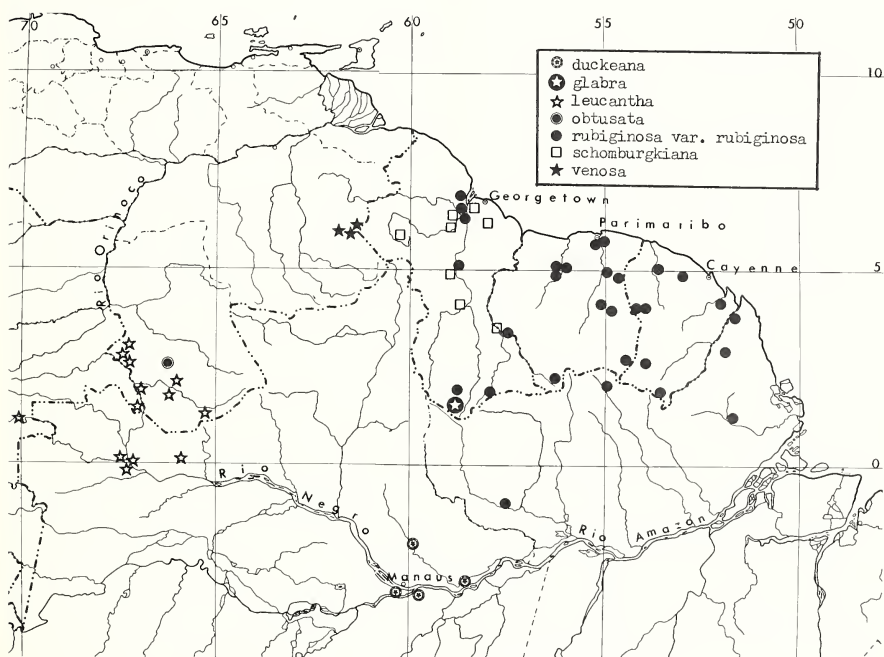
Stipules broadly oval, 20 mm long and 17 mm wide, or ovate-triangular, 4 mm long and 3 mm wide, acute; leaf rachis (11-)15-22 mm long, the leaflets 4- or 5-jugate, the blades more or less inequilateral basally, the lower side somewhat shorter and more acute, at least the upper two or three pairs; inflorescences 6.5-8.5 dm long, the pedicels mostly 2.5-3 mm in diameter; sepals 21-35 mm long, 7-15 mm wide.

TYPE COLLECTION.—*G. M. Versteeg* 48 (holotype U), "fluv. Gonini" Suriname, August 1903.

DISTRIBUTION.—Rain forest of interior Suriname at low elevations.

SURINAME: Gonini R., 25 Feb 1918, *Gonggrijp* 3700 (U); no locality, 1841, *Hostmann* 129 (BM) and 229-A (BM, G, K); Jacob Kondre, Saramacca R., 16 June 1944, *Maguire* 23804 (A, F, U, US); Coppenam R., Onobissi, 15 March 1916, *Suriname Forestry Bureau* 2577 (NY).

Hostmann 229 is the number of the type collection of *E. rubiginosa* Miquel, so the collection cited above, showing all the characters of variety *grandiflora* Pulle, will be cited with an "A" suffix to distinguish it. It surely represents a mixture of collections somewhere at some time; otherwise one must assume that there are several collections with flowers exhibiting some sort of abnormality in the typical population. Such an assumption has not been borne out by dissections of the flowers.

FIGURE 11.—Geographic distribution of several *Eperua* species.

DISCUSSION.—Until new field study brings together more adequate representation of the two forms of *E. rubiginosa*, varieties *rubiginosa* and *grandiflora* will be maintained separately. They differ in flower size and in number of pairs of leaflets. The species differs from all the others with the elongate pendent inflorescences in its unique (for this genus) multicellular, irregularly branching pubescence (Figure 1a) and from most of its relatives in having nonfalcate leaflets. It shares that characteristic with *E. glabra*, perhaps its nearest relative, which besides being almost totally glabrous has eglandular sepals. The two species also have all stamens fertile, as well as lateral (rather than intrapetiolar) stipules. The verrucose pollen of this species appears to be intermediate between the punctate-rugulose pollen of the basic stock and the punctate form of more advanced taxa.

4. *Eperua falcata* Aublet

FIGURES 5, 13

Eperua falcata Aublet, Pl. Guian. 1:369, t. 142, 1775.

Panzera falcata (Aublet) Willdenow, Sp. Pl. 2(1):540, Mar 1799.

Dimorpha falcata (Aublet) J. E. Smith in Rees, Cyclopaedia 11(2), 28 Nov 1808.

Large tree 8–40 m tall, the trunk 20–80 cm in diameter, the bark brownish-gray with rather large lenticels, the branchlets minutely puberulous, usually glabrescent and often nitid; stipules caducous, 2.5–4.5 mm long, 1.5 mm wide, triangular-lanceolate, acute, joined in a bifid, intrapetiolar stipular body, glabrous or minutely puberulous externally; petioles (23–)30–40 (–50) mm long, usually minutely puberulous, the rachis (32–)50–75 (–85) mm long, usually minutely puberulous; leaflets 3- or 4-jugate, (seedlings bijugate), the petiolules (3–)4–5 (–6) mm long, canaliculate on the upper side, minutely puberulous, sometimes glabrous or glabrescent, the blades minutely pellucid-punctate, plane, chartaceous to thinly coriaceous, glabrous, falcate-elliptic, (7–)9–12 (–15) cm long, 3–7.5 cm wide, the base usually obtuse or rounded-obtuse, infrequently acute, the apex acuminate to long-acuminate and usually mucronulate, the costa and venules prominulous; inflorescence a terminal, pendent raceme of racemes (6.5–)10–14 (–25) dm long, the axis usually glabrous except minutely strigulose in the floriferous portion, the hairlets

yellowish-brown, the lateral racemes (27–)30–50 (–100) mm long, the bracts caducous, 2–3.5 mm long and wide, broadly ovate to semicircular, strigulose externally, glabrous on inner surfaces, the bracteoles caducous, 3–4 mm long, 3–5 mm wide, broadly ovate, pubescent as bracts, arising near the base of the hypanthium; pedicels 9–18 mm long, minutely strigulose, the hypanthium 4–5 mm long, 5 (–8) mm wide, minutely strigulose externally; sepals deep red to red-brown, pink within, 16–20 mm long, 6–14 mm wide, oblong to oval-oblong, obtuse, minutely strigulose externally, glabrous within, the two outer sepals broader, cucullate; petal pink to scarlet, 13–18 mm long, 19–25 mm wide, oblate-flabelliform, basally truncate, glabrous, the 4 petalodia semicircular, 1 mm in diameter, glabrous; filaments of 4 or 5 fertile stamens pink, united with 4 or 5 sterile (the anthers smaller) ones in a villose to villose-sericeous, equilateral tube ca. 4 mm long, the filament of the one free stamen villose in the basal half, 20–30 mm long, filaments of the larger stamens 32–45 mm long, glabrous above stamen tube, smaller ones 20–25 mm long, villose, the anthers ca. 8 mm long and 3.5 mm wide, oval-oblong, glabrous; stigma capitate, the style glabrous, 40–42 mm long, the ovary oblong to oblong-obovate, 6–8 mm long, 3 mm wide, velutinous, the gynophore 2–5 mm long, puberulous to glabrous; fruits flat, somewhat arcuate-oblong, 24–36 cm long, 6.5–9.5 cm wide, minutely strigulose but eventually glabrous, the seeds flat, oval, 33 mm long, 22 mm wide, the margins incassate, the seed coat thin, red-brown, minutely tessellate.

TYPE COLLECTION.—*F. Aublet s.n.* (lectotype BM) "Cayenne 1775." The lectotype sheet has created some confusion and could easily affect the nomenclature of the species. The specimen consists of an inflorescence representing Aublet's species, unattached to vegetative material of another species altogether, probably *E. rubiginosa*. There are BM sheets collected by Martin in "Cayenne" that bear mixtures of *E. rubiginosa* and *E. falcata*, as well as several which have only material of the first of this pair. Aublet's plate and description surely represent what has been called *E. falcata* by most workers in recent generations. Thus, the lectotype must be restricted to the inflorescence on the BM sheet.

DISTRIBUTION.—Frequent to dominant in riv-

erine or low elevation, dry evergreen or swamp-woodland rain forest on a wide range of soils (often pure white sand) at elevations up to 700 m in southeastern Venezuela, central Guyana and Suriname, coastal French Guiana, and adjacent northeastern Brazil; planted in the Trinidad Botanic Gardens, Cameroon (West Africa), and in West Java in the Bogor Botanic Gardens. (The collection from the Victoria Botanical Garden, Cameroon, bears a binomial—"Eperua preussii"—which I have not found in any of the standard floras, Index Kewensis, etc. It apparently has no validity). Flowering from July to January; fruiting August to April.

VENEZUELA. Bolivar: Between El Dorado and km 88, 9 Sept 1966, *Blanco 603* (US); 90 km El Dorado toward Santa Elena, 28 Dec 1956, *Foldats 2645* (US); between kms 42 and 65, road south of El Dorado, 230 m, 26 July 1960, *Steyermark 86692* (NY, US). GUYANA: Morebo, Barima R., 11 Dec 1908, *Anderson 122* (K); Botanic Gardens, Georgetown, Oct 1904, *Bartlett 8150* (NY); upper Rupununi R., near Dadanawa, 28 May 1922, *de la Cruz 1373* (F, GH, NY, US); Essequibo-Mazaruni Divide, 2 Sept 1932, *Davis 319* (FD 2312) (K); Lima, west bank of Essequibo R., 4 May 1960, *Harris TP-404* (K); Corantijne R., Oct 1870, *Im Thurn s.n.* (K); Corantijne R., Nov 1879, *Jenman 234* (K) upper Demerara R., Sept 1887, *Jenman 4095* (K), *4101* (K), Nov 1888, *4941* (K); near Bartica, Nov 1888, *Jenman 5015* (BM); Mazaruni R., *Lang 276* (NY); Comaka, Demerara R., May 1923, *Persaud 243* (F); Mazaruni R., *Lang & Persaud 272* (F); Essequibo R., Moraballi Creek near Moraballi-Wineperu Divide, 28 Aug 1929, *Sandwith 137* (K, NY, RB, U), 23 Sept 1929, 329 (K, RB, U, US); Trail Casobrikeya to Pipilipai, Kukui R., 6 Sept 1960, *Tillett & Tillett 45304* (F, NY, RB, US); near falls of Kako R., 23 Sept 1960, *Tillett & Tillett 45413* (NY); Kamarang R., west bank above Utschi R., 550 m elev., 25 Oct 1960, *Tillett & Tillett 45791* (NY, RB) and *45794* (GH, NY, US). SURINAME: Upper Coppename R., Sept 1901, *Boon 1199* (U); Vosberg, Caronie R., 1947, *Burger 8* (U); Jodensavanne-Mapanne Creek area, 9 Dec 1963, *Elburg 9822* (U); Sarakreek, near Sinnannamary, 13 Nov 1950, J. & P. A. *Florschütz 217* (U); "Boven Para," Sept, *Focke 845* (U); no locality or date, *Hostmann s.n.* (M); Gran Rio R., 6 Sept 1910, *Hulk 227* (U); 1-5 km north of Lucie R., 3 km west of Oost R., alt 225 m, 8 Sept 1963, *Irwin et al 55448* (GH, NY, U, W); Lucie R., 2-5 km below the confluence with the Oost R., 8 Sept 1963, *Irwin et al 55467* (F, NY, RB, U, US); Zuid R., 2 km above junction with Lucie R., 15 Sept 1963, *Irwin et al 55716* (GH, NY, U, US); Fallawata 3 Nov 1971, *Jimenez-Saa 1542* (K, U), 11 Nov 1971, *1597* (K, U), 16 Nov 1971, *1622* (K) and *1625* (U), 17 Nov 1971, *1627* (K); Jodensavanne-Mapanne Creek area, Suriname R., 19 Sept 1953, *Lindeman 4649* (F, U); base of Tafelberg, 13-15 Sept 1944, *Maguire 24720* (A, F, NY, U, US) and *24778* (A, F, NY, U, US); Frederik Top, 2 km SE of Juliana Top, 700 m elev., 29 July 1963, *Maguire et al 54101* (F, G, GH, M,

NY, U); Tanjimama R., 17 Nov 1954, *Mennega 441* (U); no locality, 1850, *Miquel s.n.* (K); Mapane region, 7 Nov 1967, *Sabajo & Roberts 11192* (U); Juliana Top, 550 m, 29 July 1964, J. P. Schulz 10237 (U); no locality or date, *Schweinitz s.n.* (NY); Sectie "O," 28 Oct 1915, *Suriname Forestry Bureau 1171* (U), 7 Feb 1916, *1609* (U), 17 March 1917, *2750* (U), 26 July 1917, *3100* (U), 1 Nov 1917, *3385* (BR, U), 6 Nov 1917, *3401* (U, US), 5 Nov 1917, *3408* (NY, U), 26 Jan 1918, *3618* (K, U), 28 Jan 1918, *3625* (U), 12 Aug 1918, *3970* (BR, U, US), 17 Aug 1918, *3972* (K, U), 5 Dec 1918, *4192* (U), 9 Dec 1918, *4200* (U), 16 Sept 1919, *4416* (NY, U), 22 Dec 1919, *4528* (U), 3 Oct 1920, *4791* (U), 7 Feb 1921, *5042* (U), 3 Nov 1921, *5408* (U), 3 Nov 1921, *5420* (U), 24 Nov 1922, *5999* (U); Brownsberg, 10 Apr 1916, *Suriname Forestry Bureau 1725* (U), 10 Oct 1917, *3210* (U), 22 Nov 1917, *3434* (U), 27 Sept 1919, *4420* (K, NY, U), 15 March 1922, *4536* (U), 10 Sept 1921, *5364* (U, US), 26 Oct 1921, *5547* (U), 18 July, *6906* (BR, U); Zanderij 1, 8 Nov 1918, *Suriname Forestry Bureau 4061* (U), 28 May 1919, *4324* (U), 14 Oct 1920, *4838* (U), 27 Jan 1921, *5060* (NY, U), 28 Apr 1922, *5804* (U); Watamirij, 11 Oct 1921, *Suriname Forestry Bureau 5398* (U), 19 Dec 1921, *5549* (U); Blakhawatra, 28 Oct 1921, *Suriname Forestry Bureau 5524* (U); Litanie R., near Knopaiamoi, Dec 1903, *Versteeg 393* (U); Zanderij I, Oct. 1944, *Woodherbarium Suriname 22* (A, K, NY, U), 23 (A, K, NY, U); Sectie "O," Sept 1942, *Woodherbarium Suriname 66* (A, K, NY, U); Paramaribo, *Wulschlägel 149* (NY, W); Para, *Wulschlägel s.n.* (BR). FRENCH GUIANA: St. Laurent, Maroni R., 14-15 April 1961, *Aubreville 236* (P, U) and *260* (US); route de St. Laurent-Cayenne, km 11, 7 Aug 1953, *BAFOG 51M* (P, U); Crique Serpent, 2 Feb 1954, *BAFOG 143M* (P, U); Cayenne, Nov-Dec 1956, *BAFOG 1274* (U); plateau no. 2, carreau no. 57, route de Mana, 22 Nov 1955, *BAFOG 7062* (NY, P, U), 23 Nov 1955, *7064* (NY, P, U); St. Laurent, Feb 1956, *BAFOG 7254* (U) and *7298* (U); Charvein, Tracé de L'Acaraouy, 10 Nov 1913, *Benoist 193* (P); Charvein, 16 Jan 1914, *Benoist 596* (P); upper Maroni, 1877, *Crevaux s.n.* (P); Mana R., Crique Tamanoir, 18 Aug 1962, *Halle 579* (P); 0.5 km south of mouth of Rio Maturá, 21 Sept 1960, *Irwin et al 48408* (GH, NY, U, US); Camopi R., near junction with Oiapoque R., 2 Oct 1960, *Irwin et al 48613* (GH, NY, U, US); Maroni, Charvein, Mar 1901, *Lemee s.n.* (P); Cayenne, *Martin s.n.* (BR, K); no locality or date, *Melinon s.n.* (F, GH, K, NY, P, R, US); Balaté, St. Jean du Maroni, 23 Sept 1970, *I. Petrov 239* (P); no locality or date, *Richard s.n.* (G, W); Karouany, 1896, *Sagot 183* (BM, G, K, NY, P, W); no locality or date, *Vallant s.n.* (US); Maroni, *Wachenheim 130* (P); Godebert, *Wachenheim 405* (US). BRAZIL: Amapá: Rio Oiapoque, 19 Oct 1950, *Froes 26687* (IAN, NY, P, RB, US); edge of Rio Ingarari near junction with Rio Oiapoque, 15 Sept 1960, *Irwin et al 48277* (F, NY, US); Rio Oiapoque near Mt. Carupina, 16 Oct 1960, *Pires et al 48876* (NY, US).

LOCAL NAMES AND USES.—Apa (Irwin et al 48277), apa roxo (Pires et al 48876), baboen wabela (Woodherbarium Suriname 66), bioudou (FGFD 7062), bioulou wata (BAFOG 143M), bootlace tree (Broadway s.n., Trinidad), bylhout

(Focke 845), caraota (Blanco 603), itoeli walaba (Woodherb. Sur. 66), mahomillo negro (Steyermark 86692), rosa de montaña (Foldats 2645), sand wallaba (Harris TP-404), tamoeno pale-o (Woodherb. Sur. 23), soft wallaba (Sandwith 329), wapa gras and wapa huileux (BAFOG 1274), walaba (Broadway s.n.), walaba koeleroe (Woodherb Sur. 23), white wallaba (Davis 319), zwarte walaba (Woodherb. Sur. 22); waraba (Tillett & Tillett 45794). Used for making shingles.

DISCUSSION.—The most frequent, widely distributed species of the genus, *E. falcata*, is easily distinguished from the other two species with falcate leaflets and elongate, pendent inflorescences (*E. venosa* and *E. leucantha*). Its brownish-gold-colored, minutely strigulose inflorescences and sepals, its villous staminal tube, and its capitate stigma (rather than bilobed-capitate) serve to separate it in field or herbarium. From *E. rubiginosa*, with which it is sometimes confused, it differs, among other things, in the eglandular outer sepals; *E. rubiginosa* has an apical-dorsal gland on each of the two outer sepals. Palynologically, *E. falcata* is unique by virtue of its heterobrochate-reticulate ectexine. Although two other species, *E. purpurea* and *E. oleifera*, have pollen-ectexines that are classified as reticulate, comparison of the scanning electron micrographs (Figure 9) reveals two distinctive ectexine patterns. Taking all data into consideration, *E. falcata* is nearer the other pendent-inflorescence species, especially *E. rubiginosa*, than to the *E. purpurea*-*E. oleifera* alliance.

5. *Eperua venosa* Cowan

FIGURES 5, 11

Eperua venosa Cowan, Mem. N. Y. B. G. 10:148, 1 July 1958.

Large tree to 30 m tall and 60 cm in diameter, the branchlets glabrous; stipules persistent, rigid, connate laterally in a compound, bifid, intrapetiolar body, 4–5 mm long, ca. 2 mm wide, lanceolate-triangular, acute, glabrous externally but sericeous on the inner surface, ciliolate; leaves glabrous, lucid, the petioles (22–)32–45 mm long, the rachis 30–55 mm long, terete; leaflets bijugate, the petiolules (6–)9–13 mm long, the blades pellucid-punctate, plane, coriaceous, (11.5–)14–22 cm long, (5–)8–9 cm wide, elliptic to broadly elliptic, the apex abruptly or gradually acute to acuminate,

sometimes mucronate, the base of the lower pair rounded-obtuse, the upper pair inequilateral basally, obtuse on the lower side but attenuate-acute on the upper side, the venation prominently salient on both blade surfaces; inflorescence a pendent, terminal raceme of racemes (85–)145–188 cm long, the axes minutely puberulous, the lateral racemes 2–4.5 cm long, the bracts early caducous, about 3 mm long and 3.5 mm wide, broadly ovate, ciliolate, strigulose externally, glabrous on the inner surface, the bracteoles caducous, arising in the upper part of the pedicel, ca. 4–4.5 mm long and 4 mm wide, strongly concave, broadly ovate, pubescent as bracts; pedicels 8–15 mm long, gray-sericeous, the hypanthium 4–7 mm long, 6 mm in diameter, minutely sericeous externally, the nectaries projecting just above the hypanthium rim; sepals green with purple tint, the two outer ones broader and cucullate, 20–30 mm long, 9–13 (–17) mm wide, oblong to elliptic-oblong, obtuse, minutely sericeous outside, glabrous within; petal deep rose-colored, 25–34 mm long, 48–60 mm wide, broadly oblate-flabelliform, strigulose externally at the base, glabrous within, the four petalodia ca. 0.8 mm long and wide, semicircular, the margin crenulate; 10 stamens fertile, filaments 40–50 mm long, the staminal tube 8–10 mm long, somewhat arcuate, densely sericeous on the inner and outer surfaces, the base of the free portion of the sterile filaments also sericeous, the anthers 6.5–9 mm long, 3–3.5 mm wide, glabrous; stigma capitate, sometimes obviously bilobed, the style 45–60 mm long, glabrous except at the extreme base, the ovary oblanceolate, 8–10 mm long, 3.5–4.5 mm wide, densely pilose-sericeous, the gynophore pilose-sericeous, 3.5–6 mm long; fruit not seen.

TYPE COLLECTION.—*H. R. Kunhardt, Jr.*, 20 (holotype NY), Angel Falls, Bolívar, Venezuela.

DISTRIBUTION.—Frequent in lowland rain forest in southeastern Venezuela.

VENEZUELA. Bolívar: El Foco, Río Uirí-yuk, 30 August 1962, Maguire *et al* 53514 (NY, US); Triana Savanna, Cerro Pitón, 5 Sept 1962, Maguire *et al* 53597 (BR, NY, U, US).

DISCUSSION.—A cluster of three species—*E. venosa*, *E. leucantha*, and *E. falcata*—may have been derived from the *E. rubiginosa*-*E. glabra* group. All three have falcate leaflets and bifid, nonfoliaceous, intrapetiolar stipules. The ten fertile stamens of *E. venosa* link it to *E. rubiginosa*-*E. glabra*,

but a closer relationship is evident with *E. leucantha*, from which *E. venosa* differs in petal color (deep rose vs. white) and pubescence, as well as in number, form, and venation of the leaflets. The fine ashy puberulence of the inflorescence and sepals in *E. venosa* and *E. leucantha* contrasts with *E. falcata*, as well as with that of *E. rubiginosa*. The petal of *E. venosa* is somewhat attenuate and externally puberulous basally, rather than truncate and glabrous as in all the nearly related species. The pollens of *E. venosa* and *E. leucantha* are very similar in being the only two that are 3-porate as well as punctate-rugulose.

6. *Eperua leucantha* Benth

FIGURES 6, 11

Eperua leucantha Benth, Fl. Bras. 15(2):225, 1870.

Small to large tree (8-)12-25 m tall, (10-)50-60 cm in diameter, the bark gray, smooth, the branchlets micropuberulous at first, glabrescent; stipules deciduous, lanceolate, sometimes somewhat arcuate, joined in an intrapetiolar body 3-5 mm long, 1.5-2 mm wide, glabrous except marginally ciliate; petioles (17-)25-40(-55) mm long, glabrous or infrequently micropuberulous and glabrescent, the rachis (27-)50-95(-123) mm long, glabrous or pubescent as petioles; leaflets mostly 3-jugate, sometimes 2- or infrequently 4-jugate, the petiolules (5-)7-8(-10) mm long, usually glabrous but sometimes micropuberulous, sulcate on upper surface, the blades pellucid-punctate, (8-)10-16(-20) cm long, 3.5-7(-8.5) cm wide, chartaceous to thinly coriaceous, plane, falcate-elliptic, the base mostly rounded-obtuse or obtuse, sometimes the upper pairs acute basally, infrequently the lower side of the leaflet obtuse and the upper side attenuate-acute, the apex acuminate to long-acuminate, the tip often obtuse and usually mucronate, glabrous or rarely micropuberulous at the base of the costa on the upper surface, the venation prominulous to subobscure; inflorescence a terminal, pendent raceme of racemes (37-)60-90(-116) cm long, the main axis micropuberulous, the axis of the lateral racemes (6-)7-8(-10) mm long, microstrigulose, the bracts caducous, the bracteoles arising about midway on the pedicels, caducous; pedicels (5-)10-14(-22) mm long, micro-

puberulous to microstrigulose, the hairlets grayish, arcuate, the hypanthium (3-)4-5.5 mm long, 5-7 mm in diameter, microstrigulose externally, the nectaries slightly exerted, inconspicuous; sepals pellucid-punctate, concave, fleshy, white, oval to oblong, obtuse, two outer ones broader and cucullate, (15-)18-20(-29) mm long, 7-10(-12) mm wide, micropuberulous or microstrigulose externally, inner surfaces glabrous; petal white, 20-33 mm long, 36-55 mm wide, broadly flabelliform, basally truncate, sessile, glabrous, four petalodia 0.8-1.5(-5) mm long, 0.8-1.5 mm wide, mostly semicircular to oblate or oval; all 10 stamens apparently fertile, filaments joined at the base in a subequilateral tube 3.5 to 5 mm long, the tube and the base of shorter filaments sericeous externally and on the inner surfaces, the longer stamens 38-56 mm long, the shorter ones 30-43 mm long, the anthers 5-8 mm long, 2-3 mm wide, oval to oblong, the thecae microtessellate; stigma capitate, sometimes somewhat bilobed, the style 33-53 mm long, glabrous, the ovary sericeous-velutinous, 6-10 mm long, 3-4 mm wide, oblong-obclavate or oblong-obovate, the gynophore sericeous, 2-5 mm long; fruit 25-31 cm long, 6.5-9.5 cm wide, minutely strigulose, seeds oval, flat, 35 mm long and 21 mm wide.

TYPE COLLECTION.—*R. Spruce* 2021 (holotype K, isotypes BM, G, GH, M, P, W), "Rio Negro, moist forest at Uanauaca, Jan 52," Amazonas, Brazil.

On the holotype label, Spruce records the following:

This tree, called Jauacanã in Lingoa Geral grows throughout the Upper Rio Negro, Uaupés and Casiquiare, where along with the Jeparú (*Eperua purpurea*) it is characteristic of the caatingas, and is perhaps the more frequent of the two. It flowers nearly throughout the dry season, but is in greatest perfection in the months of September & October. No use seems to be made of any part of it, but the flowers afford a great deal of honey to bees, as do also those of two species of *Humirium* growing in the driest parts of the caatingas & flowering at the same time. When the Indians see these trees flowering copiously they predict an abundance of wild honey.

DISTRIBUTION.—Frequent in uppermost Rio Negro Basin in Brazil, west to the Río Vaupes drainage of southeastern Colombia, east and north to the Río Guainia-Río Casiquiare in southwestern Venezuela on sandy soils sometimes in savanna-border forest, at 120 to 250 m elevation;

flowering October to January; fruiting February to April.

COLOMBIA. Vaupés: San Felipe, Río Negro, 13–25 Nov 1952, *Humbert 27386 bis* (US); Río Kuduyari, 16 Oct 1952, *Schultes & Cabrera 17872* (BM, GH, NY, U, US). VENEZUELA. Amazonas: Yavita-Pimichin Trail, near Pimichin, 21 Nov 1953, *Maguire et al 36307* (NY, US); Río Yatua near Caño Tauavaca, 4 Dec 1953, *Maguire et al 36508* (F, NY); Río Yatua near Cerro de la Neblina, 3 Jan 1958, *Maguire et al 42610* (F, GH, NY, RB, U, US); San Carlos de Río Negro, 17–18 Apr 1970, *Steyermark & Bunting 102733* (US); Yavita, 23 Jan 1942, *LL Williams 13939* (A, G, RB, US); Maroa, Río Guainia, 17 Feb 1942, *LL Williams 14390* (F, G, US); Pimichin, Río Guainia, 3 Apr 1942, *LL Williams 14940* (G), 1 Apr 1942, *14942* (F, US); Capihuara, alto Casiquiare, 5 June 1942, *LL Williams 15801* (F, G, US). BRAZIL. Amazonas: São Gabriel, Río Negro, 29 Oct 1932, *Ducke 164* (A, F, NY); Río Negro above mouth of Río Curicuriary, 19 Nov 1929, *Ducke 23289* (G, RB, US); São Gabriel, upper Río Negro, 28 Oct 1932, *Ducke 23732* (P, RB, U); Porto Curucuihy, Río Negro, 6 Oct 1945, *Froes 21104* (F, IAN, NY, US); São Felipe, Río Negro, 1 Oct 1952, *Froes 25826* (IAN); Río Cauaburi, 7 Nov 1965, *Maguire et al 60130* (F, NY, US); Marabitanas, 20 Apr 1947, *Pires 481* (IAN); Río Negro-Rio Vaupés, 1 May 1947, *Pires 531* (NY, US); Río Vaupés, Taraquá, *Pires 978* (IAN); road from Camanaus to Vaupés, 30 Oct 1971, *Prance et al 15684* (GH, M, NY, U, US); Río Negro, Ilha das Flores, 8 March 1959, *Rodrigues & Pires 178* (IAN, US); upper Río Negro, Ilha das Flores, 17 Feb 1959, *Rodrigues 905* (U, US).

LOCAL NAMES AND USES.—Acanã, Iuacanã (*Rodrigues 905*), jauacanã (*Spruce 2021*), yaguana, yahuana (*LL Williams 14390*), yauacano (*Ducke 23732*). The wood is very heavy and is used locally in Venezuela for house posts and for bridges.

Some of the stamens (two to six) in flowers of *E. leucantha* do not bear fertile anthers, a characteristic shared with *E. falcata*. The white petal of *E. leucantha* contrasts sharply with all the other species with the elongate, pendent inflorescences, although less so with *E. glabra* which has a cream-colored petal. The nearest relative is unquestionably *E. venosa* which has a deep rose-colored petal with the base attenuate and puberulous externally, and ten fertile stamens. Their pollens are virtually identical (cf. discussion following *E. venosa*).

7. *Eperua duckeana* Cowan, new species

FIGURES 6, 11

Arbor parva ad mediocris 7–25 m alta, trunco 20–30 diametro, ramulis glabris et nitidis; stipulae

plerumque deciduae foliaceae glabrae, 9–15 mm longae, 9–10 mm latae, inaequilateraliter ovales ad ovatae; petioli 10–35 mm longi, glabri, rhachibus (8–)11–20 cm longis, glabris; foliola plerumque 4-jugata, petiolulis 4–8 mm longis, plerumque glabris, laminis aliquando plus minusve pellucidopunctatis, coriaceis, planis, 6.5–10 (–12) cm longis, 3–6 cm latis, plerumque uno vel duo jugis basilibus ovatis ad lanceolatis et rotundato-obtusis, reliquis jugis ellipticis et basi subobtusis ad acutis, acuminatis ad longo-acuminatis mucronulatisque, glabris aut raro micropuberulis ad basem supra, plus minusve nitidis supra, venis venulisque prominulis; inflorescentiae plerumque terminales composito-racemosae, aliquando solum racemosae, 3–8 cm longae, axe tomentuloso, pilis arcuatis bifidis, bracteae bracteolisque caducis; pedicelli 8–20 mm longi, tomentulosi, hypanthio 3–4 mm longi, tomentulosi, hypanthio 3–4 mm longo, 4–6 mm diametro, tomentuloso, nectariis super labrum hypanthii procurrentibus; sepalia diluto-viridia, tomentulosa extus, intus glabra, oblonga ad ovalia ad elliptica, 12–18 mm longa, 4–9 mm lata, uno dorsuali latiore et concavo, plerumque sepalis externis duobus glandulo versum apicem ornatis; petalum album, glabrum aut raro leviter puberulum basaliter, 14–25 mm longum, 22–35 mm latum, oblatum, truncatum ad basem, petalodiis 1–2 mm longis; omnia stamina fertilia, filamentis 26–62 mm longis, 9 tubo basaliter conjugentibus, tubo plus minusve zygomorpha, 3.5–9 mm longo, tomentuloso et glabro virgato, antheris oblongis ca. 3.8 mm longis et 1.5 mm latis, glabris; stigma capitellatum, stylo 26 mm longo, glabro, ovario oblanceolato vel oblongo-oblanceolato, 7–8 mm longo, 3–3.5 mm lato, dense tomentuloso, gynophoro 6–10 mm longo, tomentuloso; fructus tomentulosus, 16 cm longus et 6 cm latus (submaturus), oblanceolatus, planus, carpophoro ca. 20 mm longo, tomentuloso.

TYPE COLLECTION.—*A. Ducke 732* (holotype US sheet 1875576, isotypes F, NY, R) Río Urubú below Itacema Falls, Amazonas, Brazil, 7 July 1941.

DISTRIBUTION.—Primary forest on sandy or clay soil, especially along rivers, but above the annual flood levels, in the vicinity of Manaus. Flowering June to September; fruiting May to December.

BRAZIL. Amazonas, vicinity of Manaus: Reserva Florestal Ducke, 20 Sept 1968, *Aluisio 172* (INPA, US); edge of Riacho

Grande, 15 Nov 1956, *Coelho 4308* (US), 15 Nov 1956, *Dionisio* (INPA no.) 4308 (IAN); upper Mindú R., 19 Nov 1935, *Ducke 244* (NY); Estrada do Aleixo, 25 Aug 1931, *Ducke 23734* (G, P, RB, U, US); Rio Tarumã, 9 Aug 1949, *Froes 24949* (IAN); Rio Urubú, 20 Oct 1949, *Froes 25330* (IAN); Estrada BR-17, km 3, 13 June 1956, *Melo & Coelho 3913* (US); Kms 60-70 Manaus-Itacoatiara, 21 Oct 1963, *Oliveira 2737* (IAN); Estrada AM-1, km 70, 13 May 1969, *Osmarino s.n.* (INPA, US); Manaus to Caracará Road, km 26, 10 Nov 1966, *Prance et al 3072* (F, GH, NY, R, U, US); Rio Urubú between Iracema Falls and Natal, Caracará Road, 5 June 1968, *Prance et al 4977* (F, G, GH, M, NY, R, U, US); Estrada Manaus-Itacoatiara, km 202, 19 Dec 1966, *Prance et al 3720* (NY), km 69, 8 Sept 1960, *Rodrigues & Chagas 1725* (US), 5 Oct 1960, *Rodrigues et al 1807* (US), km 65, Reserva Walter Egler, 4 Feb 1970, *Rodrigues 8686* (INPA, US), km 55, 18 March 1961, *Rodrigues & Lima 2233* (INPA, US); Reserva Florestal Ducke, 1 Dec 1964, *Rodrigues & Osmarino 6769* (INPA, US); Igarapé do Riacho Grande, 14 Aug 1957, *William 501* (IAN).

DISCUSSION.—This species shares many character combinations with *E. schomburgkiana*, but there are substantial phenotypic differences. Most conspicuous of these is the pubescent ovary and smaller flowers, as well as the geographic distribution. It is named to honor Adolpho Ducke, prodigious pioneer in the collection and study of Brazilian tree legumes.

8. *Eperua glabriflora* (Ducke) Cowan, new combination

FIGURES 7, 12

Eperua bijuga Martius ex Benth. var. *glabriflora* Ducke, Trop. Woods 62:27, 1940.

Tree 5-35 m tall, the trunk 15-30 cm in diameter, the bark thin, slightly scaly, the branchlets glabrous, nitid; stipules 2-4 mm long, 2-3 mm wide, triangular to triangular-lanceolate, acute, glabrous; leaves glabrous, the petioles (12-)15-25 (-30) mm long, the rachis (30-)50-75 (-85) mm long; leaflets bijugate, the petiolules 6-12 mm long, the blades somewhat pellucid-punctate, coriaceous, sometimes rigidly so, the margins revolute, 7-20 cm long, 5-10 cm wide, the lower pair often smaller and ovate to elliptic, the upper pair elliptic, the base of all leaflets rounded-obtuse or those of the upper ones acute, the apex acute to acuminate, mucronate, nitid on both surfaces, the venation prominulous with the costa depressed on the lower blade surface; inflorescence an axillary or terminal raceme of racemes (2.5-)7-9 (-10.5) cm

long, glabrous, the bracts and bracteoles caducous, glabrous, the bracts 5.5 mm long and 6 mm wide, broadly ovate, the apex gland-tipped dorsally, the bracteoles 7.5-10 mm long, 8 mm wide, oval-ovate, acute, gland tipped dorsally near the apex; flowers glabrous except for the androecium, the pedicels 3-10 mm long, glabrous, the hypanthium 2-3 mm long, 3-5 mm in diameter, glabrous, the nectaries obvious; sepals purple, pellucid-punctate, 13-22 mm long, 3-10 mm wide, polymorphic, oval, elliptic, oblong, falcate or not, the dorsal one larger, concave, the outer two with a gland near the apex on the outer surface; petal red to purple, 4-5 cm long, 4.5-6.5 cm wide, broadly obcuneate, the base attenuate, the petalodia 0.6-1.5 mm long; stamens all fertile, 20-45 mm long, 9 united basally in an inequilateral tube 7 mm long on the shorter side and 10-12 mm long on the other, the tube puberulous externally and on the inner surfaces, the anthers oval 2.5-3 mm long and 1.5-1.7 mm wide; gynoecium glabrous, the stigma obtuse, the style 24-33 mm long, the ovary obcuneate, 4-7 mm long, 3-3.5 mm wide, the gynophore 5-9 mm long; fruits flat, woody, broadly oblong, 12.5-15 cm long, 6-10 cm wide, the dorsal margins incrassate, the carpophore 15-25 mm long.

TYPE COLLECTION.—*A. Ducke 158* (lectotype US, sheet 1693166, isotypes A, F, NY, R), Estrada do Aleixo, 3 April 1936, Amazonas, Brazil. This is one of three syntypes cited in the protologue. A second collection labeled "158 (II a Col.)" at IAN was taken at the type locality but on 25 June 1944.

DISTRIBUTION.—Common to dominant in upland, nonflooded rain forest on marshy soils of mixed sand and humus in northwestern Brazil, especially near Manaus. Flowering from February to June; fruiting July to December.

BRAZIL. Amazonas, Manaus: Estrada Manaus-Itacoatiara km 27, 7 Apr 1967, *Byron & Elias 67* (INPA, US), June 1932, *Ducke 14a* (A, F), Rio Tarumã, 7 Aug 1949, *Froes 24926* (IAN), 21 May 1903, *Goeldi 3862* (BM, G, RB, US); 12 Feb 1958, *INPA 6065* (US); Parque 10, 28 March 1958, *INPA 6280* (IAN, US); along road to Aleixo, Aug-Sept 1936, *Krukoff 8006* (BM, BR, G, GH, P, NY, U); km 202, near Rio Urubú, Itacoatiara Highway, 19 Dec 1966, *Prance et al 3709* (F, G, GH, NY, R, U, US); beside Igarapé Tarumã, 14 March 1967, *Prance et al 4637* (F, GH, NY, R, U, US); Reserva Florestal Ducke, picada PE, P.25, 26 Aug 1957, *Rodrigues 562* (US); cachoeira alta do Tarumã, 27 July 1961, *Rodrigues & Chagas 3061* (US); Reserva Florestal Ducke, near Q22, 29 Feb 1964, *Rodrigues & Osmarino 5723* (US), near Q20, 5982 (US);

Manaus, Res. Fl. Ducke, Quadrat 21, 7 May 1965, *Rodrigues & Osmarino 6932* (INPA, US); 6 Aug 1965, *Rodrigues & Osmarino 7005* (INPA, US). Para: Faro, 27 Jan 1927, *Ducke 20313* (RB, U).

LOCAL NAMES AND USES.—Muirapiranga (Ducke 158), muirapiranga da folha grande (Rodrigues & Osmarino 5982). Frequently used for firewood, particularly because the wood is resinous.

DISCUSSION.—Originally described as a variety of *E. bijuga* by Ducke, *E. glabriflora* amply deserves recognition as a distinct species by virtue of its regular hypanthium, glabrous gland-tipped outer sepals, longer bracteoles, and most obviously by the revolute leaflets. Both species have all ten stamens fertile, which character alone separates them from all the others with short, erect inflorescences except *E. schomburgkiana*, which has a white petal and more pairs of leaflets. There seems little reason to doubt the close relationship of *E. glabriflora* to *E. bijuga*, both having close affinity with *E. jenmanii*.

9. *Eperua bijuga* Martius ex Benth

FIGURES 7, 12

Eperua bijuga Martius ex Benth, Fl. Bras. 15(2):226, 1870.
Eperua bijuga Martius ex Benth forma *typica* Ducke,
Trop. Woods 62:26, 1940.

Small tree 7–12 m tall, the branchlets glabrous, shiny; stipules foliaceous, free from each other, falcate-elliptic to falcate-oval, 7–12 mm long and 3–10 mm wide, persistent, rigid, glabrous; leaves glabrous, the petioles 8–17 (–23) mm long, the rachis 25–65 mm long; leaflets bijugate, the petioles 6–13 mm long, the blades pellucid-punctate, plane, coriaceous, 9.5–20.5 cm long, 3.5–8.5 cm wide, elliptic to ovate or lanceolate, the lower pair sometimes shorter, ovate-elliptic and basally rounded-obtuse, the upper pair elliptic and basally acute, the apex acuminate or acute, sometimes bluntly so, the venation subobscure; inflorescence an axillary or terminal raceme or raceme of racemes 1.5–4 cm long, the axes puberulous, the bracts caducous, the bracteoles deciduous, obovate, 3–5 mm long, 5–8 mm wide, ciliolate, puberulous externally, glabrous within, arising about midway on the pedicels; pedicels 7–8 mm long, puberulous, the hypanthium inequilateral, 1–2 mm long, ca. 5

mm wide, the nectaries conspicuous; sepals 18–22 mm long and 10–12 mm wide, oblong-elliptic or oblanceolate-oblong, the margins scarios, puberulous externally, glabrous within; petal red, rose-purple, glabrous, 5–7.5 cm long, 6 cm wide, obcuneate-flabelliform, the petalodia 1.5–3 mm long, 0.8–1.3 mm wide; stamens all fertile, 22–45 mm long, 9 of the filaments united basally in an inequilateral tube, 12–15 mm long on the ventral side, the tube puberulous, the anthers oval, 3.5–5 mm long and 2–2.5 mm wide; gynoecium glabrous, the stigma obtuse, unilateral on the style, the latter 30–35 mm long, the ovary oblong-obovate, 8–9 mm long, 3–4 mm wide, the gynophore 7–9 mm long; immature fruits 9–10 cm long, 5–6 cm wide, subquadrate, glabrous, with a bluish bloom when immature, the carpophore 14–20 mm long.

TYPE COLLECTION.—C.F.P. *Martius s.n.* (holotype K, isotypes M), “Para, in sylvis inundatis ad insulam Marajo,” Brazil, May 1820.

DISTRIBUTION.—Occasional in the flood forest along small rivers or small streams in the area near or at the mouth of the Amazon River and in French Guiana. Flowering and fruiting April to July.

FRENCH GUIANA: No locality or date, *Lemée s.n.* (P) and *Richard s.n.* (P). BRAZIL, Terr. Amapá: Rio Apurema, 22 July 1951, *Froes & Black 27607* (IAN, NY, R). Pará: Mosqueiro, Rio Pará, 20 June 1943, *Ducke 1260* (NY, R, US); Rio Marataú (tributary of Rio Aramã), *Breves Id.*, 1 Dec 1922, *Ducke 16927* (P, RB, U); Mosqueiro, 13 Oct 1923, *Ducke 16928* (RB, U); Belém do Pará, 10 May 1923, *Ducke 16929* (P, RB); Soure (ínsula Marajo), 13 April 1927, *Ducke 20312* (RB, U, US); Rio Macacoari, Município Macapa, 5 July 1951, *Froes & Black 27281* (GH, IAN, NY, US); vicinity of Anapú, Rio Cariatuba, Portel, 17 May 1956, *Froes 32988* (US); vicinity of Anapú, Portel, 10 May 1956, *Froes 32776* (IAN), 4 Aug 1956, *Froes 32930* (IAN), 32938 (IAN), 12 Aug 1956, *Froes 32962* (IAN); vicinity of Rio Mojú, Rio Cairari, 25 March 1957, *Froes 33130* (IAN). Gurupá, *Martius s.n.* (G); Thomé Assú, Rio Acará, 27 July 1931, *Mexia 5982* (A, BM, F, G, GH, NY, U, US); Ilha do Marajo, Rio Paracaruarí, 6 Sept 1969, *Oliveira 4929* (IAN); Belém, IPEAN, Igapó do Catú, 27 May 1968, *Pires & Silva 11758* (IAN) and 3 June 1968, *Pires & Silva 11785* (IAN); Colares Island, May 1832, *Poeppig 2949* (NY, W).

LOCAL NAMES AND USES.—Fava do matto (Mexia 5982); ipê, muirapiranga (Ducke in literature).

DISCUSSION.—Both *E. bijuga* and *E. glabriflora* have petals reminiscent of those of *E. jenmanii*, from which both species may have originated,

while retaining the ten fertile stamen condition of the "ancestral" *E. schomburgkiana*. Unlike *E. glabriflora*, leaflets of *E. bijuga* are plane, the inflorescence and sepals are puberulous. The latter is typically a tree of the regularly inundated (perhaps even daily?) flood plains along the margins of small streams and rivers in the area around the mouth of the Amazon; *E. glabriflora* is a tree of the "terra firme," the land above regular flooding in northwestern Brazil, especially near Manaus.

10. *Eperua obtusata* Cowan, new species

FIGURE 11

Arbor alta, ramulis et foliis glabris; stipulae caducae, non visae; petioli 3–4.5 cm longi, valde canaliculati, rhachibus 4.5–5.5 cm longis, valde canaliculatis; foliola bijugata, petiolulis 4.5–5 mm longis, laminis minute pellucido-punctatis, coriaceis, planis, 8.5–11 cm longis, 4–5.5 cm latis, elliptico-oblongis, ad basem inaequilateralibus, plus minusve rotundato latere inferiore sed acuto latere superiore, ad apicem rotundatis, venulis prominulis, nervo marginali distincto; inflorescentiae axillares, racemosa, 7.5–9.5 mm longae, axe minute striguloso, bracteae et bracteolis deciduis, ca. 2 mm longis et 1–2 mm latis, ovatis, acutis, minute strigulosi, bracteolis prope basem pedicelli nascentibus, pedicellis 8.5 mm longis, minute strigulosi; hypanthium 2 mm longum, 3.5 mm latum, cupulare, minute strigulosum externe; sepala ad apicem conspicue glandulosa, angusto-elliptica ad elliptica, 20 mm longa, 5–8 mm lata, minute strigulosa externe; petalum oblato-obovatum, ad basem attenuatum, ca. 5 mm longum et 6.5 cm latum, petalodiis ca. 5 mm longis et 1.5–1.8 mm latis, oblongo-lanceolatis; androecium glabrum, 7 staminibus fertilibus, filamentis 11.5–26 mm longis, eis fertilium staminum longioribus, 9 in tubo inaequilaterali conjunctis 6.5 mm et 10 mm longo, antheris 3.5 mm longis, 1.5 mm latis, ovalibus, glabris; stigma truncatum, stylo 34 mm longo, glabro, ovario ca. 5 mm longo et 2 mm lato, obovato-oblongo, sericeo, gynophoro 4 mm longo, sericeo; fructus non visus.

TYPE COLLECTION.—*Ll. Williams 16183* (holotype US sheet 1834953) Capihuara, Río Casiquiare, Amazonas, Venezuela, 3 Oct 1943.

DISTRIBUTION.—Known only from the type collection.

DISCUSSION.—In a genus of species characterized by acute to acuminate leaflets, the broadly rounded ones of *E. obtusata* are a striking contrast. No doubt it is properly referred to this genus but considerable question arises concerning its near relatives. Here I have placed it between *E. rubiginosa* and *E. schomburgkiana* with which it shares the gland-tipped sepals characteristic of the first and the inflorescence-type of the second.

11. *Eperua grandiflora* (Aublet) Benth

FIGURES 8, 12

Eperua grandiflora (Aublet) Benth, Fl. Bras. 15(2):226, 1870.

Tree 8–30 m tall, the trunk 20–40 cm in diameter, the branchlets glabrous, nitid; stipules deciduous to persistent, more or less foliaceous, rigid, glabrous, falcate-lanceolate or falcate-elliptic, or inequilaterally oval to elliptic to lanceolate, sometimes lanceolate-triangular, 4–12 mm long, 2–7 mm wide; leaves glabrous or sometimes micropuberulous on the upper surface of the base of the costa and leaflet blade, the petioles 9–21 mm long, the rachis 4.5–12.5 cm long; leaflets 3- or 4-jugate, the petiolules 4–8 mm long, the blades epunctate, rigid-coriaceous, nitid, plane or marginally revolute, all elliptic to lanceolate or frequently the lowermost pair ovate to lanceolate, (4–)7–11.5 (–15) cm long, 2–5 (–7.3) cm wide, the base of the lowest pair or of all but the terminal pair rounded-obtuse, the others acute to attenuate-acute, the apex acute to long-acuminate, mucronulate, the venation prominulous to subobscure; inflorescences axillary racemes of racemes 3–10 cm long, the axes minutely puberulous, the bracts broadly ovate, 2–4 mm long, 3–4 mm wide, ciliolate, minutely puberulous externally, the bracteoles 3–4 mm long, 3–5 mm wide, broadly ovate, imbricate, clasping the upper part of the pedicel and the hypanthium base, pubescent as the bracts, arising at or near the pedicel-apex, usually at slightly different levels; pedicels 4–5.5 mm long, minutely puberulous, the hypanthium inequilaterally cupular, 1–1.5 mm long, 2.5–4 mm in diameter, minutely pu-

berulous externally, the nectaries projecting above the hypanthial rim; sepals oblong to elliptic, 10–12.5 mm long, 2–6 mm wide, minutely puberulous externally, the dorsal one concave and larger; petal pale pink or lavender-pink, more or less flabelliform, 2.5–3.5 cm long, 2.5–4.5 cm wide, glabrous, the petalodia 0.8–2 mm long, 0.4–0.8 mm wide; 4 or 5 of stamens with larger anthers, the filaments of 9 united in an inequilateral tube 3–5 mm long on the shorter side, 5–6.5 mm on the longer, the filaments 15–30 mm long, puberulous in the united region but mostly glabrous above, the anthers oval, 1.8–2.5 mm long, 1–1.5 mm wide, more or less puberulous or glabrous; stigma obtuse, the style 19–28 mm long, the ovary obovate, 3–5 mm long, 1.5–3 mm wide, densely pilosulose or glabrous, the gynophore 3–5 mm long, pilosulose or glabrous; fruits not seen.

**11a. *Eperua grandiflora* (Aublet) Benth
guyanensis Cowan, new subspecies**

FIGURE 12

A ssp. *grandiflora* foliola marginibus revolutis minute venulosus, antheris aliquando leviter minuteque puberulis, ovario gynophoroque dense pilosuloso differt.

TYPE COLLECTION.—*T. G. Tutin 245* (holotype US sheet 1743474, isotypes BM, K, U), 83 mi Bartica-Potaro Road, Guyana, 23 June 1933.

DISTRIBUTION.—Central to south-central Guyana in low forest on white sands.

GUYANA: Along Berbice-Rupununi Cattle Trail, Berbice or Demerara County, 20 May 1919, *Abraham 133* (K, NY); Essequibo-Mazaruni Divide, 0.5 m S of Bartica, 2 Sept 1932, *Davis 317* (FD 2310) (K) and *318* (FD 2311) (K); upper Rupununi R., near Dadanawa, 24–29 July 1922, *de la Cruz 1704* (GH, NY, US); Moraballi Creek, 11 Nov 1940, *Fanshawe 605* (FD 3341) (K, NY); branch of Eberobo R., Berbice Co., 20 May 1919, *Hohenkerk 788* (K); Essequibo R., opposite Bartica, Nov 1886, *Jenman 2482* (K, NY); no precise locality or date, *Jenman 6269* (K, NY); Great Falls, Demerara R., March 1898, *Jenman 7304* (K); Essequibo R., Moraballi Creek, near Bartica, 20 Sept 1929, *Sandwith 314* (K, NY, RB, U); no locality, 1844, *Rich. Schomburgk 988* (1722) (BM, G, GH, K, P, W).

LOCAL NAMES AND USES.—Ituri wallaba (Sandwith 314); yoboko wallaba (*Hohenkerk 788*). Used for firewood.

**11b. *Eperua grandiflora* (Aublet) Benth
ssp. *grandiflora***

FIGURE 12

Parivoa grandiflora Aublet, Pl. Guian. 2:756, pl. 303, 1775.
Dimorpha grandiflora (Aublet) Willdenow, Sp. Pl. 3(2):971, 1–10 Nov 1802.
Eperua kourouensis Benoist in Lecomte, Not. Syst. 3:273, 7 May 1917.

Leaflets plane; anthers and gynoecium glabrous.

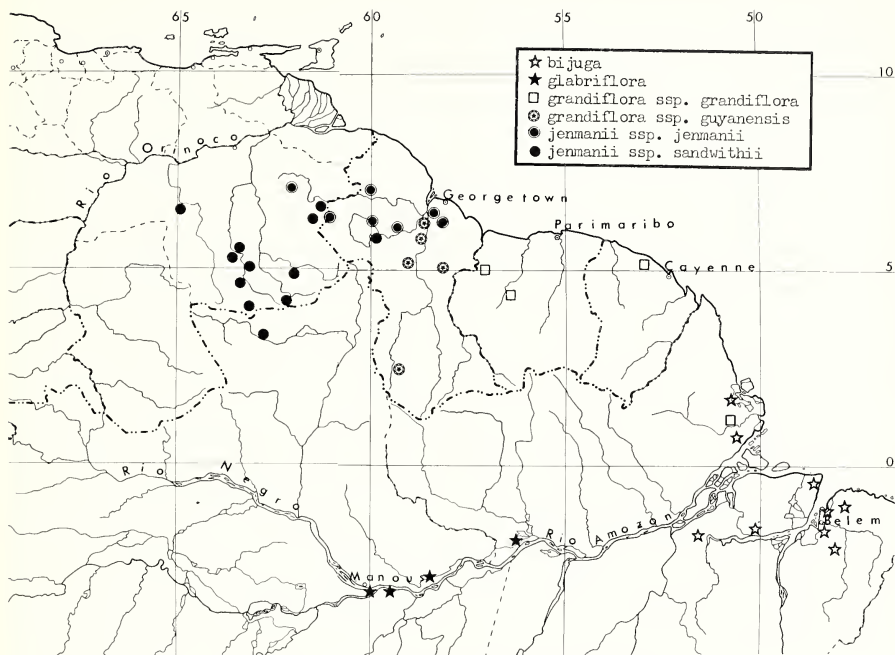
TYPE COLLECTION.—*F. Aublet s.n.* (holotype BM) "ad ripas fluviorum Guianae," French Guiana.

DISTRIBUTION.—Frequent in forest along Rio Araguari on Brazil-French Guiana Border, coastal French Guiana and south-central Suriname.

SURINAME: Upper Coppename R., Oct 1901, *Boon 1209* (U); Fallawatra, 18 Jan 1972, *Jimenez-Saa 1698* (K). FRENCH GUIANA: Gourdonville, Kourou R., 8 Sept 1914, *Benoist 1595* (P) (type of *E. kourouensis* Benoist). BRAZIL: Terr. Amapá, Rio Araguari: 2 Sept 1961, *Pires et al 50673* (F, NY, R, U, US), 12 Sept 1961, *Pires et al 50878* (GH, NY, RB, U, US), 29 Sept 1961, *Pires et al 51307* (G, NY, U, US); vicinity of Piedra Fina, 10 Oct 1961, *Pires 51659* (F, GH, K, NY, U, US).

DISCUSSION.—This is one of the frequently misinterpreted species in the genus, largely because of the specific epithet. For a species characterized by a petal among the smallest in the genus, "grandiflora" seems entirely inappropriate. However, compared to the second species of Aublet's genus *Parivoa* (a synonym of *Eperua*), which belongs to another genus altogether, the flower is enormous so the name must have seemed distinctive. The epithet has often been attached to collections of *E. jenmanii* just because of the large flowers of the latter.

It is still a rather poorly known species throughout its range, especially surprising in view of its frequency in the boundary area between Brazil and French Guiana, as well as in the coastal plain of the latter country. It apparently is derived from *E. jenmanii* from which it differs most obviously in flower size and petal shape. The two constituent subspecies differ in leaflet details, pubescence of the ovary, and geographic range. In addition, some collections of ssp. *guyanensis* have flowers whose anthers are sparsely puberulous, but this is neither very easily observed nor is it always true.

FIGURE 12.—Geographic distribution of several *Eperua* species.

12. *Eperua jenmanii* Oliver

FIGURES 8, 12

Eperua jenmanii Oliver, Hooker's Icones 20:1955, 1891.*E. stipulata* Kleinhoonte, Rec. Trav. Bot. Neerl. 30:171, 1933
[identity questionable since type is sterile, probably juvenile foliage].

Medium to large tree 10–35 m tall, the trunk 15–70 cm in diameter, the branchlets glabrous, nitid; stipules glabrous, rigid-foliaceous, free from each other or united laterally near their base, 3–25 mm long, 1.5–14 mm wide, lanceolate to ovate, falcate, acute to acuminate or rounded; petioles (8–)14–23 (–45) mm long, glabrous, the rachis (4.5–)8–15 (–21) cm long, glabrous; leaflets 3- to 5-jugate, sometimes the upper ones bijugate, the petiolules 4–7 (–12) mm long, glabrous or sparsely

micropuberulous, the blades pellucid-punctate or epunctate, plane to narrowly revolute, coriaceous, sometimes thinly so, 6–13 (–18) cm long, 3–8 cm wide, the basal pair ovate to lanceolate, the other pairs elliptic, the base rounded-obtuse, frequently cordulate, the apex acuminate to long-acuminate, mucronate, the blades glabrous or micropuberulous on the upper surface at the base, the venation prominulous; inflorescence a simple axillary or terminal raceme, rarely with a few racemose branches, the axes 2–6 cm long, glabrous or micropuberulous, the bracts persistent, 2–5 mm long, 3–6 mm wide, broadly ovate or oval, glabrous or minutely puberulous externally, glabrous within, often ciliolate, the bracteoles persistent, 3–7 mm long, 3–7 mm wide, broadly ovate or oval, clasping the upper part of the pedicel and base of the hy-

panthium, glabrous or minutely puberulous externally, often ciliolate, arising on the pedicels near their base or up to their middle; pedicels 4.5–10 mm long, sparingly micropuberulous, the hypanthium inequilaterally cupular, 2–3.5 mm long, 5–7 mm in diameter, glabrous or micropuberulous sparingly on the outer surfaces; sepals 13–28 mm long, 5–12 mm wide, narrowly oblong-elliptic to elliptic, elliptic-oblong or oblong, glabrous or micropuberulous externally, the dorsal one broader, concave; petal dark lavender to orchid-purple with darker purple and white markings, basally white, 5–10 cm long, 4–8.5 cm wide, broadly obovate, glabrous, the petalodia 2–10 mm long, linear, oblong or triangular-lanceolate; stamens white, 4–8 apparently fertile (the anthers oblong-oval, larger), the filaments of all ten stamens joined basally in an inequilateral pilosulose tube 5–13.5 mm long on the shorter side, 8–18 mm long on the longer, the dorsal free stamen 32–35 mm long, the others 18–65 mm long, most of filaments pilosulose basally, glabrous above, the anthers oval, apiculate, 2–4.5 mm long, 1–2.5 mm wide, glabrous; gynoecium glabrous, the stigma obtuse to capitate, the style white, 39–54 mm long, the ovary 5–6.5 (–10) mm long, 3–3.5 (–5) mm wide, obovate, the gynophore 6–11 mm long; fruits flat, woody, oblong to broadly oval, 13–22 cm long, 7–13 cm wide, the dorsal margin incrassate, the seeds oval, 3.5–5.5 cm long, 2–5 cm wide, pale brown or nitid-red-brown.

12a. *Eperua jenmanii* Oliver ssp. *jenmanii*

FIGURES 2c–e and 12

Stipules 3–9.5 (–20) mm long, 1.5–5 (–10) mm wide; leaflets pellucid-punctate; bracts, bracteoles, inflorescence axes, and hypanthium minutely or microscopically puberulous, the bracts 4–5 mm long, 4.5–6 mm wide, the bracteoles 5–7 mm long and wide; staminal tube 9.5–13.5 mm long on shorter side, 12–18 mm on the longer side.

TYPE COLLECTION.—*G. S. Jenman 2154* (lectotype K), Essequibo River, Aug 1884, Guyana, Dec 1899. In the protologue, Oliver listed five Jenman collections of which the one named above is an adequate representative.

DISTRIBUTION.—Frequent to common in lowland

rain forest, often along rivers, in French Guiana, Guyana (on coarse white sands in the Pakaraimas) and in southeastern Venezuela at 250–550 m elevation; probably also in Suriname but fertile material from there has not been seen that can be assigned for certain to this species; cultivated in Mexico, Singapore, Cameroon (Africa), Jamaica, and Trinidad. Flowering August to November.

VENEZUELA. Bolivar: road south of El Dorado, 42–65 km, 26 July 1960, *Steyermark 86665* (NY, US). GUYANA: Kumaka, Kurupung R., 25 Aug 1925, *Alston 313* (K); no locality or date, *Appun 756* (K); Kartabo Point, Mazaruni R., no date or collector, *FD 958* (K); Rockstone, 15 July to 1 Aug 1921, *Gleason 837* (BM, GH, NY, US); Demerara R., Dec 1899, *Jenman 573* (K, NY), Jan 1882, *Jenman 975* (K), Apr 1887, *Jenman 3830* (K), Sept 1887, *4258* (K); Bartica, Nov 1888, *Jenman 4770* (K); Kamakusa, 9 Nov 1922, *Lang 70* (K, NY, US), 9 Nov 1922, *Lang & Persaud s.n.* (F); Moraballi Creek near Bartica, Oct 1929, *Sandwith 710* (K, NY); Kukui R., Trail from Casobrikeva V, near Adaro R. mouth to Pipilipai V, 6 Sept 1960, *Tillett & Tillett 45305* (NY, US); Kako R., 21 & 25 Sept 1960, *Tillett & Tillett 45474* (GH, NY, US); Kamarang R., at mouth of Utschi R., 20 Oct 1960, *Tillett & Tillett 45699* (NY, RB); Cuyuni R., Akarabice Creek, 31 July 1933, *Tutin 439* (BM, K, US); 8.5 miles east of Kaburi R., Mazaruni R., 20 April 1926, *Wood 876* (K). FRENCH GUIANA: no locality or date, *Martin s.n.* [type of *Dimorpha grandiflora* (Aublet) Rudge] (BM).

LOCAL NAMES AND USES.—Ituri wallaba (*Tutin 439*); mahomillo (*Steyermark 86665*), wobai-yek (*Alston 313*). The wood is used for firewood and for shingles. Oliver records the following in the protologue: "The scraped root is used by the Indians for the cure of toothache. The timber is used for the frames of houses, vat staves, paling staves, and shingles for colonial use and exportation."

DISCUSSION.—Rudge (*Trans. Linn. Soc. 9:180, 1808*) took up Aublet's *Parivoa grandiflora* for this species; it is clear from the specimens on which Rudge reported his "new species" to the Linnean Society, as well as from the description and plate, that he grossly misinterpreted Aublet's concept, which he explicitly states he is clarifying. The *Martin* collection is the only record of this species in French Guiana and probably came from some locality in the interior not collected subsequently. The specimens all show bijugate leaves, rather than 3- to 5-jugate ones, but Rudge says that the lower leaves are 3- or 4-jugate. There is somewhat more puberulence on the hypanthium/sepals but within the range of variation in the species.

**12b. *Eperua jenmanii* Oliver *sandwithii* Cowan,
new subspecies**

FIGURE 12

A var. *jenmanii* stipulis plerumque 7–25 mm longis, 4–14 mm latis, foliolis epunctatis, bracteis et bracteoleis inflorescentiarum axibus pedicellis hypanthio glabris, bracteis 2–3 mm longis et 3–4 mm latis, bracteolis 3.5–5.5 mm longis et 3–5 mm latis, tubo filamentorum 5–11 mm longo dorsaliter sed 8–15 mm longo ventraliter differt.

TYPE COLLECTION.—Bassett Maguire 33136 (holotype NY, isotypes F, GH, RB, US), Raudal Guainima, 200 m elev., 16–19 January 1952, Bolívar, Venezuela.

DISTRIBUTION.—Frequent in riverine forest from south-central to southeastern Venezuela to Guyana and adjacent northern Brazil, at 110 to 1000 m elevation. Flowering and fruiting more or less simultaneously throughout the year.

VENEZUELA. Bolívar: Río Auacapa, 22 Aug 1954, *Bernardi 1536* (NY); between El Dorado and km 88, 9 Sept 1966, *Blanco 598* (NY, US); Río Tonoro, Alto Río Paragua, 2–15 Aug 1943, *Cardona 818* (F, NY, US); mouth of Río Carapo, alto Río Paragua, 5 Sept 1943, *Cardona 985* (US); Río Ikarú, Oct 1947, *Cardona 2158* (US); Río Paragua, Guainima, 14–15 Apr 1943, *Killip 37477* (US); Río Cuyuni, 10–15 km below Cerro Escalera, 17 Aug 1962, *Maguire et al 46734* (NY, US); Río Tiricá, lower slopes of Chimantá tepui (Torono-tepui) 1000 m elev., 24 May 1953, *Steyermark 75337* (NY); Río Caroní between mouth of Río Aparurén & Uriman, alt. 400 m, *Steyermark 76074* (NY); 3–4 km SE of "Los Patos," 30 km S of El Manteco, 9 Aug 1960, *Steyermark 87075* (NY); Sierra Ichun, along Río Ichun, 29 Dec 1961, *Steyermark 90416* (US) and 30 Dec 1961, *90458* (NY, US); Río Paramichi, between mouth of Río Paramichi & Salto de Halimano, 8–9 Jan 1962, *Steyermark 90724* (NY, US). GUYANA: Demerara R., March 1898, *Jenman 7305* (K); Membaru-Kurupung Trail, 2 Nov 1951, *Maguire & Fanshawe 32435* (NY). BRAZIL: Terr. do Roraima: vicinity of Uaiça airstrip, Río Uraicoeira, 7 March 1971, *Prance et al 10871* (K, NY, U, US).

LOCAL NAMES AND USES.—Concha de suela (Blanco 598); opai-yek (Maguire 46734).

DISCUSSION.—The most conspicuous characteristic of *E. jenmanii* is its large petal, the largest in the genus; only *E. bijuga* and *E. glabriflora* compete for this distinction, but both of these have only bijugate leaflets and all ten stamens fertile. Petal size also separates *E. jenmanii* from *E. grandiflora*, which are even more closely related. The four species form a natural assemblage palynologi-

cally, all having unspecialized punctate pollen grains.

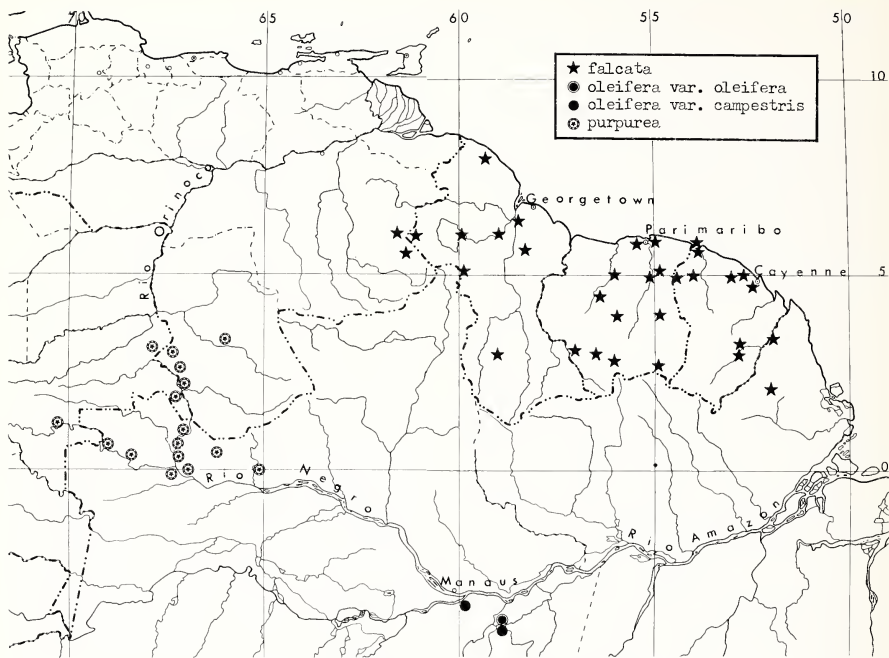
The two subspecies are separable, in addition to geography, by presence or absence of puberulence on the inflorescence and the size of bracts; the stipules tend to be larger and the staminal tube shorter in subspecies *sandwithii*. The name of the latter commemorates the name of one of the most astute legume taxonomists in botanical history. His review of the *Eperua* species that occur in Guyana is basic to the present study.

13. *Eperua purpurea* Benth

FIGURES 2a–b, f–h, 9, and 13

Eperua purpurea Benth, Fl. Bras. 15(2):226, 1870.

Large tree (15–)20–50 (–70) m tall, the trunk columnar, 30–100 cm in diameter, the bark smooth gray, gray-black, or light sand-colored, the branchlets usually glabrous, rarely micropuberulous; stipule more or less fused in one intrapetiolar body, persistent to deciduous, broadly semicircular-ovate, 2–4 mm long and wide, ciliolate, usually glabrous externally, more or less sericeous on the inner surface; petioles 10–35 mm long, glabrous, the rachis glabrous, 13–80 mm long; leaflets 2- or 3-jugate, the petiolules (3.5–)5–7 (–9) mm long, glabrous, the blades pellucid-punctate, thinly to rigidly coriaceous, the margins plane or narrowly revolute, thicker than the remainder of the blade, glabrous, (4.5–)6–10 (–11.5) cm long, 3–6 cm wide, ovate to oval or elliptic, sometimes only the basal pair ovate and the others elliptic, the base rounded-obtuse, sometimes slightly cordate, the apex bluntly acute to acuminate, often slightly retuse at the tip, the upper surface glabrous, lucid, the lower rarely microstrigulose, densely ceriferous except on the thickened marginal vein, the wax bodies contiguous, minute, the venation obscure; inflorescence a mostly terminal, infrequently axillary, raceme of racemes (3–)5–7 (–10) cm long, the axes glabrous or rarely micropuberulous, the bracts thin, pellucid-punctate, persistent or deciduous, 1.5–2.5 mm long, 1–2 mm wide, triangular-ovate, acute, glabrous except ciliolate, the bracteoles persistent, similar to bracts in texture, pubescence, size, and shape, pellucid-punctate, arising at slightly different levels on the pedicels about one-third to one-half the

FIGURE 13.—Geographic distribution of several *Eperua* species.

length from its base; pedicels (9-)10-15 (-24) mm long, slender, glabrous, somewhat pellucid-punctate, the hypanthium cupular, glabrous, pellucid-punctate 2-3 mm long, 2.5-5 mm in diameter, the nectaries usually conspicuous; sepals glabrous except more or less ciliolate, pellucid-punctate, elliptic to oval, 9-11.5 mm long, 4-9 mm wide, the dorsal one broader, concave and cucullate; petal deep rose, pink-purple, purple, rose-purple, 2.5-4.5 cm long, (3.5-)4.5-6.5 cm wide, flabelliform, shortly attenuate basally, glabrous, the petalodia 0.5-0.7 mm in diameter, semicircular; stamens 10, 3 to 5 fertile, the filaments of 9 joined in an inequilateral villose tube 4-5.5 mm long on the shorter side, 5-8 mm on the longer side, the filaments of the fertile stamens 18-35 mm long, glabrous in the upper half, the sterile ones 12-27

mm long, villose almost to apex, the one free stamen with the filament 14-15 mm long, villose, the fertile anthers oval, 2 mm long, 1.5 mm wide, glabrous; gynoecium glabrous, the stigma capitate or capitate, the style 25-35 mm long, the ovary 3-4 mm long, 1.5-2 mm wide, obovate, the apex truncate, the gynophore 2-3.5 mm long; fruits 15-17 cm long, 6-8 cm wide, oblong, flat, with a bluish bloom when young, the dorsal margins alate, the seeds flat, oval, lucid, red-brown.

TYPE COLLECTION.—*R. Spruce* 2577 (holotype K, isotypes BM, BR, F, G, GH, NY, P, RB, W) Panuré, Rio Negro-Rio Uaupés, Amazonas, Brazil, Sept 1852.

DISTRIBUTION.—Frequent to dominant in Savanna-scrub, "moist places of the upland rain forest" (Ducke, 1940) in the Rio Negro Basin of

northwestern Brazil, and in similar areas in adjacent southeastern Colombia and southwestern Venezuela at 120–750 m elevation. Flowering most heavily in October and November; fruiting November to June.

COLOMBIA. Vaupés: Río Negro, San Felipe 13–25 Nov 1952, *Humbert 27386* (US), 24 Oct 1952, *Schultes et al 17955* (BM, BR, GH, NY, U, US); Río Guainía, Caño del Caribe between Isla del Venado and San José, 2 Nov 1952, *Schultes et al 18268* (GH, U, US); Cerro de Tipiaca, between Mita and Javareté on Río Vaupés, 14–24 May 1953, *Schultes & Cabrera 19324* (GH, NY, US). VENEZUELA. Amazonas: Yavita, Río Atabapo, 19 Oct 1950, *Maguire 29311* (NY, RB); Playa Alta, Río Cunucunuma, 9 Nov 1950, *Maguire et al 29486* (F, NY, US); 1 km east of Maroa, 120–140 m elev., 25 Nov 1953, *Maguire et al 36398* (NY); just south of Maroa, Río Guainía, 28 Nov 1953, *Maguire et al 36452* (GH, NY, U, W); trail to Guzman Blanco 1–5 km SE of Maroa, Río Guainía, 9 Oct 1957, *Maguire et al 41776* (GH, NY, RB, U, US); Río Guainía, island at Las Isletas, 16 Oct 1957, *Maguire et al 41922* (F, NY, US); Yavita, 26 Jan 1942, *Ll. Williams 13990* (A, F, G, RB, US). BRAZIL. Amazonas: upper Río Negro, June 1932, *Ducke 52* (F, NY); Río Negro above Río Curicuriari, 19 Nov 1929, *Ducke 23288* (G, P, RB, U, US); Río Negro, *Ferreira s.n.* (P); Jauareté, Vaupés, Río Negro, 19 Oct 1945, *Froes 21206* (F, IAN, NY, US); Río Negro, Içana, Santana, 5 May 1947, *Froes 22317* (GH, IAN, U); Río Cauaburi between Cachoeira Jacamin and Manajós, 6 Nov 1965, *Maguire et al 60112* (F, NY, US); Río Negro-río Cauaburi, 27 Nov 1965, *Maguire et al 60421* (NY, US); Río Negro, Marabitanas, 20 Apr 1947, *Pires 468* (IAN, NY, INPA, US); Río Unciuxi, 200–300 km above mouth, 22 Oct 1971, *Prance et al 15513* (GH, M, NY, U, US); Tapuruquara, 27 Oct 1971, *Prance et al 15609* (GH, M, NY, U, US); Río Curicuriari, 22–24 Jan 1948, *Schultes & Lopez 9657-B* (GH, IAN, US); Río Negro, São Felipe, Serrinha opposite mouth of Río Issana, 4–7 Apr 1948, *Schultes & Lopez 9779* (IAN, R, US); Igarapé do Chuva, Taracua, Río Vaupés between Ipanoré and confluence with Río Negro, 12 Nov 1947, *Schultes & Pires 9066* (IAN, US); Panuré, Río Vaupés, Feb 1853, *Spruce 2577-A* (K).

LOCAL NAMES AND USES.—Cupaúba-rana (Spruce 2577), iebaru (Maguire et al 60112), iobaro (Pires 468), jébaru (Spruce 2577), pega-pega (Ll. Williams 13990), poo-koo (Schultes et al 17955), wapa (Schultes et al 17955), yeba (Schultes et al 17955), yebaro (Ducke 23288), yebero (Schultes et al 18268), yevaro (Ll. Williams 13990). Wood heavy, used for bridges and general construction. Spruce records the following information on the holotype-label:

This tree, called Jébaru by the Indians, is the loftiest tree in the Caa-tingas and their greatest ornament throughout the summer months. It is very frequent in the Río Negro and Uaupés, and when sailing on these rivers its red crown is

conspicuous from afar, wherever the ground is rising. The juice is very viscid and the Indians use it as birdlime for taking toucans and parrots. The bark is tough and does not decay under water: it is of a red colour. A strip of this bark, 30 ft. or more long, 11 or 12 inches broad & 1/4 inch thick is wrapped round a tube, 1 to 3 ft. long, formed of a portion of a young trunk of the Paxiuba palm (*Iriartea enorhiza* Mart.) in a slightly oblique direction, so as to form a widening spiral which extends considerably below the tube, & forms a musical instrument which is blown into like a trumpet and gives a deep sound that is heard from afar. These instruments, called Juruparis, or devils, are in use throughout the Uaupés (and anciently it would seem throughout the Río Negro) in the Doboxuris, or feasts, of the Indians. I cannot find that they are objects of actual adoration, but they certainly are of fear & respect, and several curious observances are connected with them.

DISCUSSION.—Everyone who has seen this species in the field, and reported on the experience, has exclaimed about the beauty of the tree in flower (see Spruce's description). The inflorescence is quite distinctive, partly because of the persistent bracts and bracteoles, but the best characteristic to separate the species from all other cogeners is the ceriferous undersurface of the leaflets. Microscopic, wax-secreting glands produce filaments of wax which cover the entire lower surfaces except for a thickened marginal vein (cf. Figures 1, 3). Although the shape and dimensions of the leaflets vary considerably, the waxy undersurfaces are always striking, and characters of the inflorescence are constant, especially the scarious-margined bracts and bracteoles. It is most closely related to *E. oleifera*, which has shorter pedicels and smaller nonalate-margined fruits. The pollen grains of the two species are very similar and unique in the genus by virtue of their reticulate (homobrochate) ectexine and broad colpi.

14. *Eperua oleifera* Ducke

FIGURES 9, 13

Eperua oleifera Ducke, Rev. Bot. Appl. & d'Agric. Trop. 12: 437, June 1932; Bull. Mus. Nat. Hist. Paris, ser. 2, 4:728, Oct 1932.

Small to large tree, the branchlets glabrous, minutely strigulose or micropuberulous; stipules persistent, joined laterally in a compound, intrapetiole body 2–4 mm long and 3–4 mm wide, broadly ovate, minutely strigulose externally, glabrous on the inner surfaces, ciliolate; petioles 13–23 mm

long, usually microscopically puberulous or strigulose, rarely glabrous, the rachis 38–60 mm long, pubescent as petioles; leaflets 3-jugate, the petiolules 4–5 mm long, sparingly microstrigulose or micropuberulous, the blades pellucid-punctate plane, thinly coriaceous to stiffly so, the margins usually with a thickened vein, glabrous or rarely microstrigulose sparsely below, 5.5–9 cm long, 3.5–6.5 cm wide, broadly ovate or oval to elliptic, the base rounded-obtuse or cordate, the apex bluntly acute to acuminate, the venation prominulous; inflorescence a terminal raceme of racemes 3–7.5 cm long, the axes minutely strigulose to tomentulose, the bracts caducous to deciduous, more or less broadly ovate, 1.5–2 mm long and wide, minutely strigulose to tomentulose externally, the bracteoles persistent at least to anthesis, 1.5–2 mm long and wide, broadly ovate to triangular-ovate, pubescent as bracts, arising near pedicel-apex; pedicels 4.5–8 mm long, minutely strigulose to tomentulose, the hypanthium 1–2 mm long, 2.5–3.5 mm in diameter, equilateral; dorsal sepal larger, concave, oval or ovate, the others narrow elliptic and the lateral two somewhat arcuate, 7–10 mm long, 2.5–5 mm wide, microstrigulose to tomentulose externally, glabrous within; petal pale lilac to rose-purple or purple, 25–40 mm long, 35–50 mm wide, flabelliform, somewhat attenuate and gibbous basally; 4 or 5 stamens apparently fertile (the anthers larger), the filaments of 9 joined in a strongly inequilateral tube 4 mm long on the shorter side and 5–6 mm long on the other side, the filaments of the fertile stamens 20–30 mm long, the sterile ones and the free stamen 12–17 mm long, the tube and the sterile one free, the filaments villose, the anthers 1.5–2 mm long, 0.8–1 mm wide, oval, those of sterile stamens smaller, malformed, glabrous, acute apically; gynoecium glabrous, the stigma obtuse to clavate or capitate, the style 20–24 mm long, the ovary obovate, 3–4.5 mm long, 1.5–2 mm wide, the gynophore 3–3.5 mm long; fruit flat, glabrous, ca. 6 cm long and 3.5 cm wide, the seed 25 mm long, 18 mm wide, glabrous, brown-black, nitid, pitted-reticulate.

14a. *Eperua oleifera* var. *oleifera*

FIGURE 13

Large forest tree with the leaflets oval to elliptic,

thinly coriaceous, the base rounded-obtuse; petal pale lilac.

TYPE COLLECTION.—*A. Ducke* 23290 (lectotype R, isolectotypes F-frag., G, NY, P, RB, U, US), Borba, Rio Madeira, Amazonas, Brazil, 16 January 1930. A lectotype choice is required because *Ducke* cited two syntypes in the protologue.

DISTRIBUTION.—Scattered individuals in non-inundated forest along the Rio Madeira and smaller streamlets in southern Amazonia, mostly on clay soils.

BRAZIL. Amazonas: Borba, Rio Madeira, 9 Nov 1935, *Ducke* 73 (US), 5 July 1936, *Ducke* 213 (A, F, NY, R, US), 7 Nov 1935, *Ducke* 235 (NY), 5 July 1936, *Ducke* 235a (NY).

LOCAL NAMES AND USES.—Jacaré copahiba (*Ducke* 23290). Resin from stems used in Brazilian Amazonia in manufacture of paints and varnishes.

14b. *Eperua oleifera* *Ducke* var. *campestris* *Ducke*

FIGURE 13

Eperua oleifera *Ducke* var. *campestris* *Ducke*, Bull. Mus. Nat. Hist. Paris, ser. 2, 4:728, Oct 1932.
E. campestris (*Ducke*) *Ducke*, Trop. Woods 62:25, 1940.

A small tree of the savannas with the leaflets broadly ovate, cordate, more rigid-coriaceous than the typical variety; petal rose-purple or purple.

TYPE COLLECTION.—*A. Ducke* 23291 (holotype R, isotypes G, NY, P, RB, U, US), Borba, Rio Madeira, Amazonas, Brazil, 17 January 1930.

DISTRIBUTION.—Frequent in southern Amazonian savannas, apparently restricted to this area.

BRAZIL. Amazonas: Borba, Campo Grande, 25 Aug 1942, *Ducke* 73-II (A, IAN, R, US); Manaus, Sept 1948, *Schultes & Lopez* 10337 (GH, IAN, NY, US).

Ducke made two collections in the Borba area which he numbered 73 (9 Nov 1935) and 73-II (25 Aug 1942). Apparently the data became confused on the labels during distribution of the duplicates, because 73-II is clearly variety *campestris* and 73 is the typical variety. The *Schultes & Lopez* collection differs primarily in that the various flower parts are minutely tomentulose, rather than strigulose as is the material from the type locality.

DISCUSSION.—The first publication of the species is incomplete and in French but, because it antedates the required Latin diagnosis, it is valid; the

longer, more complete Latin description later in the same year should be consulted to obtain a clearer idea of the taxon. Between the two publication dates he discovered a new subspecific taxon, variety *campestris*, which he described briefly in the "second protologue," and later raised it to specific level. The author was greatly impressed by the difference in stature of the two forms but, at least in the herbarium, the differences observed are of no more than varietal significance.

Although there are excellent distinguishing characters to separate *E. oleifera* and *E. purpurea*, they have a number of common features: (1) non-foliaceous intrapetiolar stipules; (2) regular hypanthium; (3) fertile stamens reduced to three to five; and (4) villose staminal tube. They differ most markedly in the ceriferous undersurfaces of the leaflets in *E. purpurea* and the glabrous ones of *E. oleifera*. They are scarcely separable palynologically (cf. discussion with *E. purpurea*).

Appendix 1: Excluded Names

- Parivoa tomentosa* Aublet, Pl. Guian. 2:759, 1775. [= *Crudia*.]
Eperua hohenkerkii Sprague ex Aitken, Trop. Woods 23:1, 1930. [Nomen nudum.]
Eperua decandra Blanco, Fl. Filip., ed. 1:368, 1837. [= *Afzelia bijuga*.]
Eperua falcata Blanco, Fl. Filip., ed. 1:369, 1837. [= *Afzelia rhomboidea*.]

Appendix 2: Lists

NUMERICAL LIST OF TAXA

1. *E. schomburgkiana* Benth
2. *E. glabra* Cowan
3. *E. rubiginosa* Miquel
 - a. *E.r.* var. *rubiginosa*
 - b. *E.r.* var. *grandiflora* Pulle
4. *E. falcata* Aublet
5. *E. venosa* Cowan
6. *E. leucantha* Benth
7. *E. duckeana* Cowan
8. *E. glabriflora* (Ducke) Cowan
9. *E. bijuga* Martius ex Benth
10. *E. obtusata* Cowan
11. *E. grandiflora* (Aublet) Benth
 - a. *E.g.* ssp. *guyanensis* Cowan
 - b. *E.g.* ssp. *grandiflora*
12. *E. jenmanii* Oliver
 - a. *E.j.* ssp. *jenmanii*
 - b. *E.j.* ssp. *sandwithii* Cowan
13. *E. purpurea* Benth
14. *E. oleifera* Ducke
 - a. *E.o.* var. *oleifera*
 - b. *E.o.* var. *campestris* Ducke

LIST OF EXSICCATAE

Figures in parentheses refer to the numbers assigned to the taxa, which are arranged numerically in the preceding list.

- Abraham, A. A.
133 (11a)
 Altson, A. H. G.
313 (12a)
 Aluisio, J.
172 (7)
 Anderson, C. W.
122 (4); 182 (1); 183 (3)
 Appun, C. F.
294 (3); 359 (1); 756 (12)
 Aublet, F.
s.n. (4); s.n. (11b)

- Aubreville, A.
236 (4); 260 (4); 313 (3a)
 BAFOG
51M (4); 143M (4); 219M (3a); 1274 (4); 7062 (4); 7064 (4); 7254 (4); 7298 (4); 7831 (3a); 7937 (3a)
 Bartlett, A. W.
8150 (4)
 Benoist, R.
193 (4); 1595 (11b)
 Bernardi, L.
1536 (12b)
 BGFD
958 (12a)
 Black, G. A.
49-8301 (3a); 54-17621 (3a)
 Blanco, C.
598 (12b); 603 (4)
 Boon, E.
1199 (4); 1209 (11b)
 Broadway, W. E.
s.n. (4)
 Burger, D.
8 (4)
 Byron & Elias
67 (8)
 Candido, J.
s.n. (3a)
 Cardona, F.
818 (12b); 985 (12b); 2158 (12b)
 Cavalcante, P.
2538 (3a)
 Coelho, D.
4308 (7); 5212 (1)
 Crevaux, I.
s.n. (4)
 Davis, T. A. W.
317 (11a); 318 (11a); 319 (4); 394 (1); 404 (3a)
 de la Cruz, J. S.
1373 (4); 1704 (11a); 2091 (1); 2172 (1)
 Dionisio
4308 (7)

- Ducke, A.
14a (8); 52 (13); 73 (14a); 73-II (14b); 158 (8); 164 (6); 213 (14a); 235 (14a); 235a (14a); 244 (7); 732 (7); 1260 (9); 9022 (3a); 16927 (9); 16928 (9); 16929 (9); 20312 (9); 20313 (8); 23288 (13); 23289 (6); 23290 (14a); 23291 (14b); 23732 (6); 23734 (7); 23289 (6)
- Elburg, J.
9822 (4)
- Fanshawe, D. B.
605 (11a); 644 (1); 2104 (3a)
- Ferreira, A. R.
s.n. (13)
- Florschütz, J. & P. A.
217 (4)
- Focke, H. C.
845 (4)
- Foldats, E.
2645 (4)
- Froes, R. L.
481 (6); 21104 (6); 21206 (13); 22317 (13); 24926 (8); 24949 (7); 25330 (7); 25698 (3a); 26638 (3a); 26639 (3a); 26649 (3a); 26687 (4); 32776 (9); 32930 (9); 32938 (9); 32962 (9); 32988 (9); 33130 (9); 27281 (9); 27607 (9)
- Geay, F.
s.n. (3a)
- Gleason, H. A.
332 (1); 412 (1); 837 (12a)
- Goeldi, A.
1158 (3a); 3862 (8)
- Gonggrijp, J. W.
2577 (3a); 3700 (3b); 5515 (3a)
- Guppy, N. G. L.
198 (3a); 430 (2)
- Halle, F.
579 (4); 732 (3a)
- Harris, S. A.
TP-404 (4)
- Hitchcock, A. S.
17089 (1)
- Hohenkerk, L. S.
122-B (3a); 788 (11a)
- Hostmann, F. W.
129 (3b); 229 (3a); 229-A (3b); s.n. (4)
- Hulk, J. F.
227 (4)
- Humbert, H.
27386 (13); 27386 bis (6)
- Im Thurn, E. F.
s.n. (4)
- INPA
6065 (8); 6280 (8)
- Irwin, H. S.
47471 (3a); 48277 (4); 48408 (4); 48613 (4); 55448 (4); 55467 (4); 55716 (4); 57579 (3a)
- Jenman, G. S.
234 (4); 573 (12a); 627 (1); 768 (3a); 786 (3a); 975 (12a); 1147 (3a); 1336 (1); 2154 (12a); 2482 (11a); 3830 (12a); 4095 (4); 4101 (4); 4258 (12a); 4770 (12a); 4941 (4); 5015 (4); 5257 (1); 6269 (11a); 7304 (11a); 7305 (12b)
- Jimenez-Saa, H.
1542 (4); 1597 (4); 1622 (4); 1625 (4); 1627 (4); 1698 (11b)
- Kappler, A.
1689 (3a)
- Kegel, H.
872 (3a)
- Killip, E. P.
37477 (12b)
- Krukoff, B. A.
8006 (8)
- Kunhardt, H. R., Jr.
20 (5)
- Lang, H.
70 (12a); 276 (4)
- Lang, H., & Persaud, A. C.
272 (4); s.n. (4)
- Lanjouw, J.
738 (3a); 1209 (3a)
- Lanjouw, J., & Lindeman, J. C.
324 (3a)
- Leblond, J. B.
s.n. (3a)
- Lemee
s.n. (4); s.n. (9)
- Leprieur, F.
s.n. (3a)
- Lindeman, J. C.
4649 (4); 6344 (3a)
- Linder, D. H.
132 (3a)
- Luetzelburg, P.
20211 (3a); 20399 (3a)
- Maguire, B., & Maguire, B., et al.
23804 (3b); 24720 (4); 24778 (4); 29311 (13); 29486 (13); 33136 (12b); 36307 (6); 36398 (13); 36452 (13); 36508 (6); 41776 (13); 41922 (13); 42610 (6); 46734 (12b); 53514 (5); 53597 (5); 54014 (3a); 54401 (4); 60112 (13); 60130 (6); 60421 (13)
- Maguire, B., & Fanshawe, D. B.
32435 (12b)
- Martin, P. S.
s.n. (4); s.n. (12a); s.n. (3a)
- Martius, P.
s.n. (9)
- McInon, M.
s.n. (4)
- Melo, F.
3913 (7)
- Monnaga, A. M. W.
102 (3a); 441 (4)
- Mexia, Y.
5982 (9)
- Miquel, F. A. W.
s.n. (4)
- Myers, J. G.
5672 (3a)

- Oliveira, E.
2737 (7); 4929 (9)
- Osmarino
s.n. (7)
- Perrottet, G. S.
23 (3a); s.n. (3a)
- Persaud, A. C.
14 (1); 166 (1); 243 (4)
- Petrov, I.
239 (4)
- Pires, J. M.
468 (13); 531 (6); 978 (6); 48849 (3a); 48876 (4); 50673 (11b);
50878 (11b); 51182 (3a); 51307 (11b); 51501 (3a); 51659 (11b)
- Pires, J. M. & Silva
11758 (9)
- Poeppig, E.
2949 (9)
- Poitau, A.
s.n. (3a)
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- Rech
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- Richard, L. C. M.
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- Rombouts, H. E.
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- Sagot, P. A.
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- Sampaio, A. J.
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- Sandwith, N. Y.
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- Schomburgk, Richard
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- Schomburgk, Robert
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- Schultz, J. P.
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- Schweinitz, L. D.
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- Smith, A. C.
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- Spruce, R.
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